The Taxonomy of the Salpidae (Tunicata) of the Central Pacific Ocean[1]

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INTRODUCTION

Knowledge of the salps of the central Pacific Ocean is scanty as heretofore they have been studied only in conjunction with extensive collections, such as those of the "Challenger" and "Albatross" (Herdman, 1888; Metcalf, 1918), from large areas. The present paper, which is limited to a discussion of taxonomy and morphology, is based on large collections that have recently become available. A further report on distribution and ecology is in preparation.

Although much of the present paper is of necessity similar to previously published work, especially those portions describing muscle arrangement, the descriptions are based on original study unless otherwise stated. A new method of study for salps, also applicable to many other planktonic animals, was used and is here described.

Species of the genus *Salpa* were arranged into a number of related subgenera by Metcalf (1918) as follows: *Cyclosalpa*, *Brooksia*, *Apsteinia*, *Salpa*, *Ritteria*, *Thetys*, *Pegea*, *Traustedtia*, *Thalia*, and *Iasis*. Some of these names originated with earlier investigators. Because of prior usage, it was necessary to replace *Ritteria* by *Ritteriella*, and *Apsteinia* by *Ihlea*, which he did in 1919. All these subgenera were raised to the rank of genera by Ihle and Ihle-Landenberg (1933), who at the same time added the genus *Metcalfina* for *Salpa hexagona* Quoy and Gaimard, 1824. This classification is in general use today and is followed here, with the addition of the genera *Helicosalpa* (Todaro, 1902) for *Cyclosalpa virgula* Vogt, 1854, and *C. komaii* Ihle and Ihle-Landenberg, 1936, and *Weelia* gen. nov., for *Salpa cylindrica* Cuvier, 1804. In addition, the subfamilies Cyclosalpinae and Salpinae are newly recognized here.

References included in the specific synonomies are as inclusive as possible since 1912. Additional citations prior to that date are given in detail by Ihle (1912). Only a few of the older reports (previous to 1893) have been examined, thus all citations in the synonymies previous to 1912 have been taken from Ihle unless stated otherwise.

Acknowledgments

Dr. R. W. Hiatt suggested the study and has offered his help whenever needed. I wish to express my thanks for his patient criticism of the investigation in all aspects. I wish also to state my thanks to Dr. L. D. Tuthill who helped solve many problems of a systematic nature and criticized other aspects of the

[1] Contribution No. 53, Hawaii Marine Laboratory. A portion of a thesis submitted to the Department of Zoology and Entomology, University of Hawaii, in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Manuscript received August 6, 1953.

study. Especial thanks are due Dr. P. B. van Weel who informed me of the effectiveness of toluidin blue as a stain for salps.

Mr. O. E. Sette, in charge of the Pacific Oceanic Fishery Investigations of the United States Fish and Wildlife Service (referred to in the remainder of this report as POFI), kindly permitted me to use the plankton samples of POFI. In addition, Mr. J. E. King of POFI was helpful in the final judgment as to which plankton samples would be used, as well as in obtaining the samples.

The figure of *Thetys vagina* agg. (Fig. 23*b*) was drawn by Mr. James Park, illustrator of the Department of Zoology and Entomology, University of Hawaii.

MATERIALS AND METHODS

The animals used were taken from a large series of plankton captures made by POFI (principally from cruise 5 of the "Hugh M. Smith"). The area of capture extended from 27°N. to 5°S. and from 176°W. to 155°W.

The animals were studied by staining with toluidin blue. Apparently the idea of staining the animals has not been used by anyone previous to this report except Berner (1954), who used rose bengal.

Salps cannot be advantageously stained in an alcoholic stain, as alcohol dehydrates the test. Some water-soluble stains (such as rose bengal) were found to be rather effective, but they did not result in good differentiation between test and other body structures. P. B. van Weel suggested the use of toluidin blue, which he had used on salps as a vital stain and which, he had found, differentiated between body tissues and test of the living animal. It has proved a most important contribution to this study.

Toluidin blue can be mixed in any water medium, whether it contains formalin, is salty, or is fresh. The dry stain was sprinkled into the fluid until the latter became a deep blue or purple color. The most satisfactory strength is 0.15 gram stain to 500 cubic centimeters water. The animal was placed in the stain from 5 to 30 minutes. While it was in the stain, a small pipette or hypodermic needle was used to inject stain through the mouth or cloacal opening in order to stain body tissues; this is an essential step of the staining process. When body muscles and other internal organs became rather dark, the animal was washed in a vessel containing clear water to remove excess stain. It was then ready for study, best done with a white background, but a black background or even removal from the water may be useful. There are, however, two disadvantages to the use of the stain: (1) it is not permanent in the preservative, and (2) the natural coloration of the animal becomes obscured. The many advantages of the stain, however, greatly outweigh these disadvantages.

Some salps, such as the solitary forms of *C. bakeri*, *C. floridana*, and *H. komaii*, require a different method than the one just described. In the first two species, the muscles are so delicate that they do not stain well at the usual concentration; in the latter species the test absorbs stain heavily, thereby obscuring structures beneath it. The animals were placed in clear water, *not* in the stain. Then a stain of 1 gram to 500 cubic centimeters of water was injected slowly into the body cavity until it was completely filled, and left until the muscles became dark. In this way, the test is not stained, but the body structures are.

Toluidin blue differentiates by staining the test pink and the body tissues varying degrees of blue. Thus the test and various organs of the body become completely visible and yet retain their transparency to a large degree.

Stiasny (1926) reported that the test is useful in combination with other structures, especially muscles, for distinguishing species. However, extensive examination of the stained tests shows that in the aggregate form there is often no basic type of test. It is apparently not as useful as he thought, as I found great variation in test structure of both solitary and aggregate forms.

In many species, the presence of depressions and elevations is entirely accidental, due probably to the convulsive contractions of the muscles at death. In my opinion the presence of elevations and depressions in a soft test (with the exception of distinct ridges and grooves) is in general without value as a character for species determination. There do seem to be a few exceptions, however, i.e., *Pegea confoederata* and *Ritteriella amboinensis* agg.

The asymmetric nature of aggregate individuals of salps is shown not only in the arrangement of muscles, attachment organs, and end projections but also in the sculpture of the test when it is stiff and has permanent structures (Stiasny, 1926; Ihle, 1937–39).

In some species, such as *Thalia democratica*, there are two basic body forms: one has a relatively thick test, prominent ridges and grooves, and wide muscle bands; the other has a thin test, ridges weak or absent, nonpermanent elevations and depressions, and narrow muscles.

Van Beneden and de Selys-Longchamps (1913) (*fide* Stiasny, 1926) and Stiasny showed that there had been entirely too much reliance on muscle arrangement for differentiating the various species. Nevertheless, muscle arrangement is one of the most important recognition features. In order to determine some species, however, it must be combined with other features.

MORPHOLOGY

With the exception of Traustedt (1885), Brooks (1893), van Beneden and de Selys-Longchamps (1913) (*fide* Brien, 1948), and Stiasny (1919, 1926), all investigators have described the test only incidentally, their work being primarily concerned with the muscular arrangements of the various species. The only considerable contribution to the knowledge of test structure was made by Stiasny (1926). As he showed, the great difficulty encountered in the study of the test is its almost complete agreement in refractive index with water. Some salps have tests with ridges and grooves that can be seen under water, but the test of most shows little or no opacity. Hence, almost all investigators have completely disregarded the test in their researches. Traustedt (1885) and Brooks (1893) described the test in a few species, and Brooks recognized a basic plan in the test that fits some salps, especially the solitary forms. This plan was named Brooks' rule (Regel von Brooks) by Stiasny (1926), and he applied it to many forms. Stiasny also clarified the rule and stated it as follows:

> . . . finden wir regelmässig in der Mitte der Dorsalseite eine (tiefe) Längsfurche, beiderseits begrenzt von vorspringenden kiel-ännlichen Kanten, an den seiten des Mantels vorspringende scharfe Kanten oder Flügelartige Verbreiterungen; auf der Ventralseite ist die Testa dick, mit einem medianen und 2 lateralen Kielen.

Stiasny also set up a scheme of nomenclature for test structure which is followed here although some of his terms have been changed. The result is a combination of his terms, of those used by Delage and Hérouard (1898), and some additions. It is believed that the terminology used here is both clearer in meaning and easier for use in descriptions. The resulting scheme is shown in Figure 1.

The following terms are used to describe the test:

test—the outer tunic or covering over the epidermis

mantle—the epidermis and associated tissues; the term does not refer to the test

ridge—a distinct elongate bulge, triangular in cross section

groove—a distinct elongate, angular invagination

elevation—a rounded, elongate bulge

depression—a rounded, elongate invagination

swelling—a prominent, nonelongate, rounded bulge

cavity—any concavity of the internal surface of the test

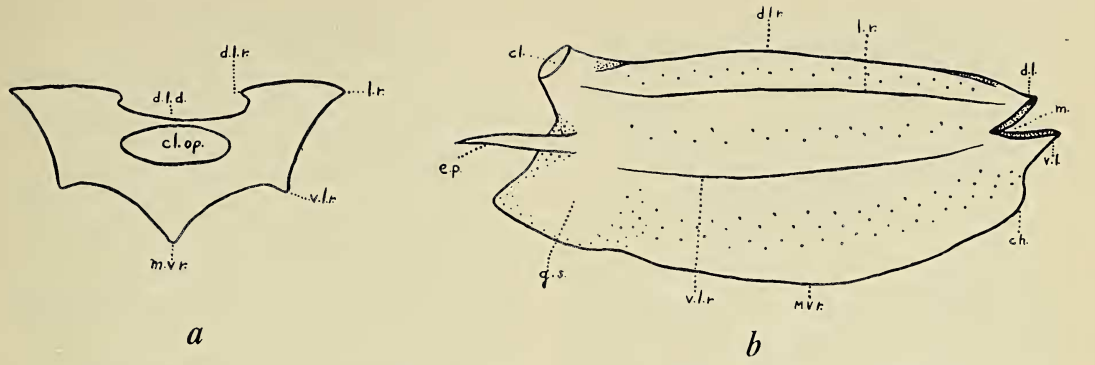


FIG. 1. Scheme of the test of a solitary form. *a*, End aspect (after Stiasny, 1926); *b*, lateral aspect (modified after Delage and Hérouard, 1898). *ch*, Chin; *cl*, cloacal opening; *dl*, dorsal lip; *dld*, dorsal longitudinal depression; *dlr*, dorsal limiting ridge; *ep*, end projections; *gs*, gut swelling; *lr*, lateral ridge; *m*, mouth; *mvr*, midventral ridge; *vl*, ventral lip; *vlr*, ventrolateral ridge.

chin—the swelling on the ventral anterior surface below the ventral lip

spine—a small, conical protrusion beyond the test margin

projection—a large protrusion of the test; it is never filamentous but may contain a mantle projection

tentacle—a filamentous protrusion of the test; it usually contains a mantle projection

sucker—a disc-like enlargement at the end of the mantle (epithelial) tube in the projections of some forms (e.g., *Thalia democratica*, sol.)

Furthermore, when the terms "ridge," "groove," etc., are used, they always refer to longitudinal ridges and grooves unless stated otherwise.

The general morphology of salps is schematized in Figure 2 to identify structures in the remaining figures. Body muscles are designated by Roman numerals from anterior to posterior (M III = body muscle three), whereas mouth and cloacal muscles are designated by letters (A, B, C, and x, y, z, respectively). This notation follows that set up by Streiff (1908) as used by Ihle (1935, 1937–39), except cloacal muscles are denoted by lowercase letters to avoid confusion with body muscles.

In addition to those listed in Figures 1 and 2, the following abbreviations are used in the other figures: *ant*, Anterior; *bl.f*, blood-forming organ; *bm*, "baumförmiger Fortsätze"; *bv*, blood vessel; *cir.pr*, circular projection; *cl.fl*, cloacal flap; *cr*, crest (dorsal limiting ridge); *dle*, dorsal limiting elevation; *dlp*, dorsolateral projection (atrial palp); *d.ten*, dorsal tentacle; *el.c*, elaeoblast cavity; *em*, embryo; *f*, fold in bottom of pharynx; *hft*, attachment organ; *ho*, hook; *in*, independent muscle; *lo*, light organ; *lpp*, lateral posterior projection; *mdr*, middorsal ridge; *mvp*, midventral projection; *ob.gr*, oblique groove; *ob.r*, oblique ridge; *pa*, test patch; *ped*, peduncle; *pl.pr*, posterolateral projection (tentacle); *pr*, posterior ridge; R, right side; *rec*, rectum; *sn*, snout; *st.at*, attachment organ; *st.op*, opening for stolon; *tes*, testis; *tr.d*, transverse depression; *vle*, ventrolateral elevation; *vlp*, ventrolateral projection; *vr*, ventral ridge.

Most drawings in this paper do not show oral or cloacal muscles, as these are small and difficult to place correctly in a drawing of the whole animal. They are described and figured for most species by Streiff (1908), Metcalf (1918), Ihle (1935, 1937–39), and Thompson (1948).

It is probable that further study will show that the attachment organs are of considerable taxonomic importance. They are only incidentally described in this paper.

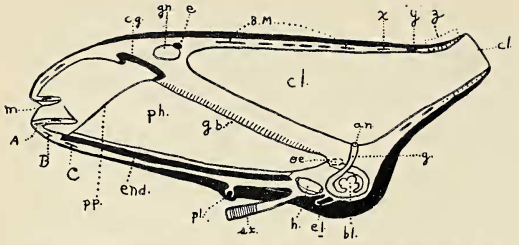


FIG. 2. Schematic median section of a solitary salp (after Ihle, 1935). A, Velum muscle; *an*, anus; B, lip muscle; *bl*, blind sac (caecum of gut); BM, body muscles; C, bow (intermediate) muscle; *cg*, ciliated groove (dorsal tubercle); *cl*, cloaca and its opening; *e*, eye; *el*, elaeoblast; *end*, endostyle; *g*, gut (intestine); *gb*, gill bar; *gn*, ganglion; *h*, heart; *m*, mouth; *oe*, esophagus; *ph*, pharynx; *pl*, placenta; *pp*, peripharyngeal band; *st*, stolon; *x*, first cloacal muscle; *y*, second cloacal muscle; *z*, third cloacal muscle (composed of a series of small sphincters).

KEY TO WORLD SPECIES AND REPRODUCTIVE FORMS OF SALPIDAE

1. Gonads present; stolon absent; eggs or embryos usually present.....aggregate (gregarious) form.....2

   Gonads absent; stolon usually present; eggs and embryos absent.....solitary (oozooid, asexual) form.....22

2(1). Intestine straight, anteriorly directed; one light organ present laterally between M II–III (there may be another between M III–IV).....**Cyclosalpa pinnata**

   Intestine neither straight nor anteriorly directed; no light organ present.....3

3(2). Two posterior projections present, containing testis and a caecum, respectively.....**Cyclosalpa bakeri**

   One or no posterior projection present.4

4(3). Testis spherical.**Helicosalpa komaii**

   Testis not spherical.....5

5(4). Posterior appendage containing testis present.....6

   Posterior appendage containing testis not present.....7

6(5). Testis projects dorsolaterally within posterior test projection.....**Helicosalpa virgula**

   Testis projects ventroposteriorly within posterior swelling.....**Cyclosalpa floridana**

7(5). Gut forms a broad loop with central space empty; a peduncle present.....**Cyclosalpa affinis**

   Gut either tightly looped or with central space filled; peduncle absent.....8

8(7). Some body muscles form complete rings.....9

   No body muscles form complete rings.....10

9(8). Body muscles fused into a single unit dorsally and ventrally.....**Brooksia rostrata**

   Body muscles not fused into a single dorsal and ventral unit; however, M II and III are rings...**Ihlea magalhanica**

10(8). All body muscles interrupted dorsally.....**Thetys vagina**

   Some or all body muscles continuous dorsally.....11

11(10). M I interrupted dorsally.....**Iasis zonaria**

   M I continuous dorsally.....12

12(11). Four symmetrical attachment organs project from each side of body.....**Pegea confoederata**

   Attachment organs either asymmetrical or not projecting beyond test outline.13

13(12). One elongate tentacle projects posteriorly from each lateroposterior angle of body.**Traustedtia multitentaculata**

   No elongate tentacle as above (short attachment organs may project laterally from the posterior region of *Thalia democratica* agg.).....14

14(13). Ventral lip sphincter 4(Mb_3) interrupted.....**Salpa fusiformis**

   Ventral lip sphincter 4 continuous, if present.....15

15(14). Muscles arranged in groups of 3 and 2 dorsally.....16

Muscles arranged in groups of 4 and 2, 4 only or 2 only dorsally 18

16(15). Gut within a broad pointed or rounded median posterior projection; ciliated groove bears a ventral languet 17

Posterior projection not containing gut; ciliated groove without languet . . . . . **Weelia cylindrica**

17(16). M III is formed of 8 or 9 fibers (Apstein, 1906*a*) . . **Thalia longicauda**

M III is formed of 3 fibers (Apstein, 1906*a*) . . . . . **Thalia democratica**

18(15). M II extends beyond endostyle to between M V–VI of opposite side . . . . . **Ihlea punctata**

M II not as above 19

19(18). Posterior projection extends beyond cloacal opening 20

Posterior projection does not extend beyond cloacal opening . . . . . **Metcalfina hexagona**

20(19). Independent muscle small, inconspicuous; M I–II narrowly fused dorsally; spaces between transverse ribs of gill bar less than 0.5 width of bar . . . . . **Salpa maxima**

Independent muscle large, conspicuous; M I–II widely fused dorsally; spaces between transverse ribs of gill bar greater than 0.5 width of bar 21

21(20). Dorsal lip sphincter 1 (M A_1) interrupted middorsally . . . . . **Ritteriella picteti**

Dorsal lip sphincter 1 continuous middorsally . . . . . **Ritteriella amboinensis**

22(1). Intestine accompanies gill bar 23

Intestine does not accompany gill bar 28

23(22). Ventral longitudinal muscle present 24

Ventral longitudinal muscle absent . . 25

24(23). A single dorsal longitudinal muscle present, connecting M I with M x on each side . . . . . **Helicosalpa komaii**

Two dorsal longitudinal muscles present, connecting M I with M VI on each side . . . . . **Helicosalpa virgula**

25(23). M I–IV fused ventrally into a single mass . . . . . **Cyclosalpa floridana**

M I–IV not fused ventrally 26

26(25). Three to five light organs present on each side of body 27

Not more than one light organ present on each side of body . **Cyclosalpa affinis**

27(26). M VI forming 2 anteriorly directed dorsal longitudinal muscles . . . . . **Cyclosalpa bakeri**

M VI forming one fused, anteriorly directed dorsal longitudinal muscle, or none . . . . . **Cyclosalpa pinnata**

28(22). A muscular snout projects anteriorly beyond mouth opening . . . . . **Brooksia rostrata**

No muscular snout projects anteriorly 29

29(28). Body muscles interrupted dorsally 30

Body muscles continuous dorsally . . 31

30(29). A long projection extending posteriorly from both posterolateral angles of body; test spiny . . . . . **Thetys vagina**

No such projections present; test smooth . . . . . **Iasis zonaria**

31(29). Some body muscles form complete rings 32

All body muscles interrupted ventrally 36

32(31). Longitudinal muscles present on each side of body, internal to body muscles . . . . . **Ihlea punctata**

Longitudinal muscles absent 33

33(32). A long projection extending posteriorly from each posterolateral surface of body 34

No such projections present 35

34(33). M I–III and IV–V forming groups dorsally . . . . . **Thalia democratica**

All body muscles separate, parallel (Traustedt, 1885) ..... **Thalia longicauda**

35(33). Not more than first four body muscles forming complete rings ..... **Ritteriella amboinensis**

M I–VI forming complete rings (Thompson, 1948) ..... **Ihlea magalhanica**

36(31). Intestine straight, extended posteriorly ..... **Ritteriella picteti**

Intestine coiled, not extended 37

37(36). Projections of test or tentacles extending beyond body outline 38

No projections of test extending beyond body outline 39

38(37). Two posterior projections present; 9 to 13 body muscles present, asymmetrical ..... **Metcalfina hexagona**

No posterior projections but with two to many tentacles; body muscles few (5), symmetrical ..... **Traustedtia multitentaculata**

39(37). Four body muscles present ..... **Pegea confoederata**

More than 4 body muscles present .. 40

40(39). Elaeoblast or its cavity present in mature specimens; ciliated groove forming a loop ..... **Salpa maxima**

Elaeoblast present only in embryos; ciliated groove simple in immature specimens 41

41(40). M I–IV converging to form a group ..... **Weelia cylindrica**

M I–III and VIII–x converging, or are parallel ..... **Salpa fusiformis**

Family SALPIDAE

The definition of the family by Ihle (1935) is followed here chiefly.

Planktonic Thaliacea with main body axis longitudinal, covered with a transparent test. Mouth opening anterior, cloacal opening posterior, dorsal or terminal. Body musculature consists of usually ventrally interrupted muscles but may include complete rings or dorsally interrupted muscles as well. Special mouth and cloacal musculature present. Pharyngeal and cloacal cavities separated by a "gill bar" lying between two large gill slits; gill bar extending from anterodorsal surface to esophagus located posteroventrally. An alternation of generations exists between the sexual blastozooid (aggregate or gregarious form) and the asexual oozooid (solitary form). The oozooid bears ventrally a proliferating stolon on which the blastozooids arise. The blastozooid produces one or several embryos on the cloacal wall which become oozooids.

The family Salpidae consists of two distinct groups of genera. I propose to give these groups the status of subfamily: the Cyclosalpinae including *Cyclosalpa* and *Helicosalpa*, the former being the type genus, and the Salpinae including all other genera of the Salpidae, *Salpa* being the type genus.

CYCLOSALPINAE subfam. nov.

The subfamily Cyclosalpinae may be distinguished by the following characteristics: (1) in the solitary form, the intestine accompanies the gill forward, being united with it over most of its length; (2) there are light organs present in all solitary forms except *C. affinis*, and here one is probably present (see description); (3) in the aggregate form, the gut is either an extended tube or a loosely formed loop, never a compact "nucleus"; (4) the aggretate forms are attached by a single peduncle or by a single large attachment process.

Genus Cyclosalpa Blainville, 1827

Solitary form with six body muscles, gregarious form with four. In the solitary formt longitudinal muscles absent or, if present, no, continuous with M I. Intestine coursing obliquely with gill bar in the solitary form, but not forming a rectum. Intestine either straight or forming an open circle in the aggregate form. Only one attachment organ, the pe-

duncle, present in the aggregate form. Body muscles penetrating into peduncle. Groups of blastozooids forming whorls on stolon.

Four species: *Cyclosalpa pinnata* (type), *C. affinis*, *C. floridana*, and *C. bakeri*.

Cyclosalpa pinnata (Forskål) 1775
Fig. 3*a–d*

Salpa pinnata Forskål, 1775: 113.
Biphora pinnata Bruguiére, 1789: 180.
Salpa pelasgica [?] Bosc, 1802: 181.
Salpa cristata Cuvier, 1804: 366.
Salpa thalia [?] Lamarck, 1816: 119.
Salpa caudata [?] Lamarck, 1816: 119.
Salpa (Cyclosalpa) pinnata Blainville, 1827: 108; Metcalf, 1918: 9; Sewell, 1926: 68; Stiasny, 1926: 414.
Salpa cyanea [?] Chiaje, 1828: 63.
Salpa proboscidalis Lesson, 1830: 95.
Salpa mucosa [?] Costa, 1839: 225.
Orthocoela pinnata Macdonald, 1864: 181.
Cyclosalpa pinnata Herdman, 1888: 87; Ihle, 1935: 527–529; Tokioka, 1937: 219; Thompson, 1948: 103.
Cyclosalpa polae Sigl, 1912*a*: 66; 1912*b* (*fide* Ihle and Ihle-Landenberg, 1937); Fedele, 1926, 1933 (*fide* Ihle and Ihle-Landenberg, 1937); Ihle and Ihle-Landenberg, 1937: 1.
Cyclosalpa bakeri Bomford, 1913: 243.
[non] *Cyclosalpa bakeri* Ritter, 1905: 54.
Salpa (Cyclosalpa) pinnata polae Metcalf, 1918: 26; Sewell, 1926: 68; Komai, 1932: 69.
Cyclosalpa pinnata polae Ihle, 1935: 527–529.
Cyclosalpa pinnata var. *polae* Tokioka, 1937: 220.

SOLITARY FORM: Four specimens examined with length range of 4–12 mm. (Fig. 3*c*,*d*). *Test:* Rather thin, glutinous, without definite elevations or depressions. Median dorsal ridge described by Stiasny (1926) absent as are anterior "ventral languets" shown by Metcalf (1918). *Muscles:* Six body muscles, each interrupted dorsally and ventrally; oral muscles touching M I. *Ciliated groove:* An arched U in dorsal view, but may be sinuous or convoluted according to various investigators.

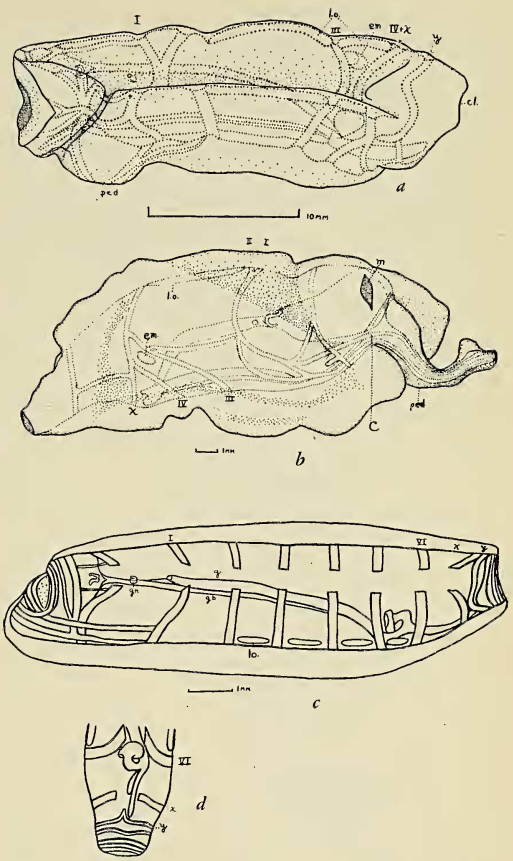


FIG. 3. *Cyclosalpa pinnata*. *a*, Aggregate form, left dorsal side; *b*, aggregate form, right dorsal side; *c*, solitary form, left side; *d*, solitary form, ventral view of cloacal region.

Viscera: Esophagus opening between M VI and x on right side, connecting to intestine which accompanies gill antero-obliquely; at junction of intestine and esophagus, two caeca projecting posteriorly, the left one almost twice the length of the right one; light organs four on each side, between muscle bands II–x (five according to most investigators, but Sewell, 1926, found only four—none between I–II—and this is also true of POFI specimens).

AGGREGATE FORM: Four specimens examined with length range of 11–31 mm. (Fig. 3*a*,*b*). *Test:* Thin and flabby, far separated from mantle except at region of mouth and cloacal openings; glutinous; no definite

elevations or depressions; peduncle long in small (*C. p. polae?*) specimens (Fig. 3*b*), much shorter in largest specimen (Fig. 3*a*). *Muscles:* Four body muscles; M I–II fused dorsally, III, IV, and x approaching or fusing dorsally; mouth muscles joining M I; bow muscles (C) forming anterior peduncle muscles on each side, M I and II fusing ventrolaterally to form posterior peduncle muscles. Thus, a total of four peduncle muscles present. *Ciliated groove:* Simple or U-shaped, located vertically. *Viscera:* Esophagus opening at level of junction of M III–IV–x; a single, posteriorly directed caecum, intestine coursing anteriorly beneath endostyle, anus opening at region of M II–III, but in larger specimen at region of M I; testis prominent, longitudinally plicated, arising at junction of esophagus and intestine, accompanying intestine anteriorly, opening by small duct slightly posterior to anus; embryo near M III or between M III–IV dorsally; one light organ on each side between M II and III—there may be two, as shown in Fig. 3*a* and as shown by Ihle (1910), Komai (1932), and Tokioka (1937); examples previously described with two pairs of light organs, as the present specimen, always large (length of specimen, 28 mm.), so this condition probably due to age.

The form (species, subspecies, variety) *polae* has been distinguished from *C. pinnata* chiefly by the following characteristics in the gregarious form (Ihle and Ihle-Landenberg, 1937); length of body, length of peduncle, relationships of M III and IV dorsally, shape of ciliated groove, eye, caecum (blind sac), and position of anus. There are evidences, however, chiefly from Sewell (1926), that this form is not distinct from *C. pinnata*. The separation dorsally of M III and IV is found in *C. pinnata* as well as in animals fitting the description of *C. polae* (Metcalf, 1918; Sewell, 1926; Komai, 1932). The ciliated groove intergrades between the form *polae* and the type (Sewell, 1926). The solitary form of *C. polae* is distinguished (Sigl, 1912*a*) by the middorsal fusion of the two M VI and their continuance as a band forward. This character apparently intergrades but should receive further study. Sewell (1926) stated:

> Had I been dealing solely with examples of the aggregated zooid I should have had no hesitation in referring this form to the subspecies *polae* but, as I have already shown, the asexual generation [of the Indian form] must be referred to *C. pinnata.* It is impossible, therefore, to distinguish *Cyclosalpa polae* from *C. pinnata* even as a sub-species, and much less, as Sigl originally claimed, as a species.

Ihle and Ihle-Landenberg (1937), however, critically studied specimens of the aggregate zooid of both forms and concluded that the two forms should be considered distinct species, as Sigl (1912*a*) had regarded them.

I have had only typical specimens of the solitary zooid of *C. pinnata* and thus can add nothing which might help settle this problem. The aggregate zooids of the POFI collections, however, show intergradation in the dorsal separation of M III–IV and structure of the ciliated groove. Tentatively, I follow Thompson (1948) in regarding the form *polae* as simply showing differences attributable to changes occurring with increasing size and believe that its recognition as a subspecies or species is probably not justified. Doubtless, the answer to the problem lies in a study of various-sized solitary forms.

An embryo was found in a collection containing aggregate forms that fit the description of *C. polae* (Fig. 3*b*). This embryo, however, is evidently a typical *C. pinnata* as the two M VI do not fuse dorsally. It was not attached to its mother, so I cannot relate it directly to the form *polae*.

Cyclosalpa affinis (Chamisso) 1819
Fig. 4 *a*, *b*

Salpa affinis Chamisso, 1819: 11.

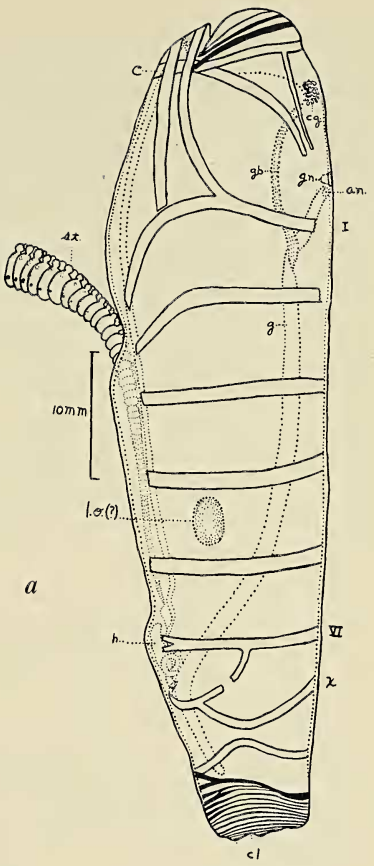
Cyclosalpa affinis Blainville, 1827 [*fide* Ritter, 1905]; Ihle, 1935: 527–529; Tokioka, 1937: 221; Thompson 1948: 108.

Salpa pinnata var. [?]Quoy and Gaimard, 1834: 582.

Salpa chamissonis Brooks, 1893: 376.
Salpa (*Cyclosalpa*) *affinis* Apstein, 1894*b*: 4; Metcalf, 1918: 27; Sewell, 1926: 74; Komai, 1932: 70.

SOLITARY FORM: One specimen examined with length of 54 mm. (Fig. 4*a*). *Test:* Thin, glutinous, attached at mouth and cloacal opening; no definite elevations or depressions. *Muscles:* Six body muscles: M I and II interrupted dorsally and ventrally, M III–VI interrupted ventrally, continuous dorsally; x sending one branch anteriorly (broken in this specimen) which is continuous with posterior branch of M VI; x continuing far ventrally; x and y converging laterally but not touching; M I joining mouth muscles. *Ciliated groove, ganglion and eye:* Ganglion and eye anterior to M I, just above anus; ciliated groove far anterior to them, highly convoluted. *Viscera:* Esophagus forming a spiral at ventral level of M VI and x; a single posterior caecum (actually double, appearing single, according to Komai, 1932) connecting to intestine which courses antero-obliquely with gill; anus opening just anterior to M I; gill ending anterior to M C; a large oval body located on each side between M IV and V. It is conspicuous with stain and probably is a light organ (this is not mentioned in past descriptions).

AGGREGATE FORM: Three specimens examined with length range of 18–33 mm. (Fig. 4*b*). *Test:* Closely attached at mouth, cloacal opening, on peduncle and intestine (Metcalf, 1918, figures it as very loose on latter two structures); test with no definite elevations or depressions, glutinous, thin, may be far separated from mantle; peduncle short, broad. *Muscles:* Four body muscles; all interrupted ventrally, continuous dorsally and separated from one another except IV and x; M I joining with mouth muscles; M C forming anterior peduncle muscles, posterior peduncle muscles independent; total of four muscles in peduncle, two anterior and two posterior; M I sending off two anterior branches; x and



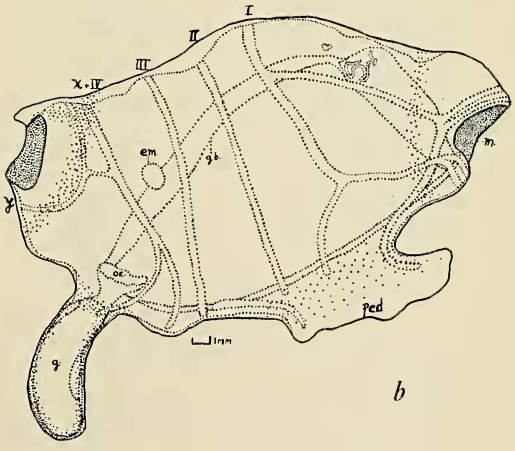


FIG. 4. *Cyclosalpa affinis*. *a*, Solitary form, left side; *b*, aggregate from, right side.

y connected by a laterodorsal branch. *Ciliated groove:* Anterior to M I, highly convoluted. *Viscera:* Gut a large open loop, forming a posteroventral evagination beyond body outline; testis contained in gut loop; embryo on right side between M III and IV; no light organs.

Cyclosalpa floridana (Apstein) 1894
Fig. 5*a*, *b*

Cyclosalpa dolicosoma-virgula Traustedt, 1893: 5.
[non] *Salpa virgula* Vogt, 1854: 11.
Salpa floridana Apstein, 1894*b:* 9.
Cyclosalpa floridana Brooks, 1908: 75 [*fide* Sewell, 1926]; Ihle, 1935: 527–529; Ihle and Ihle-Landenberg, 1935: 21; Thompson, 1948: 111.

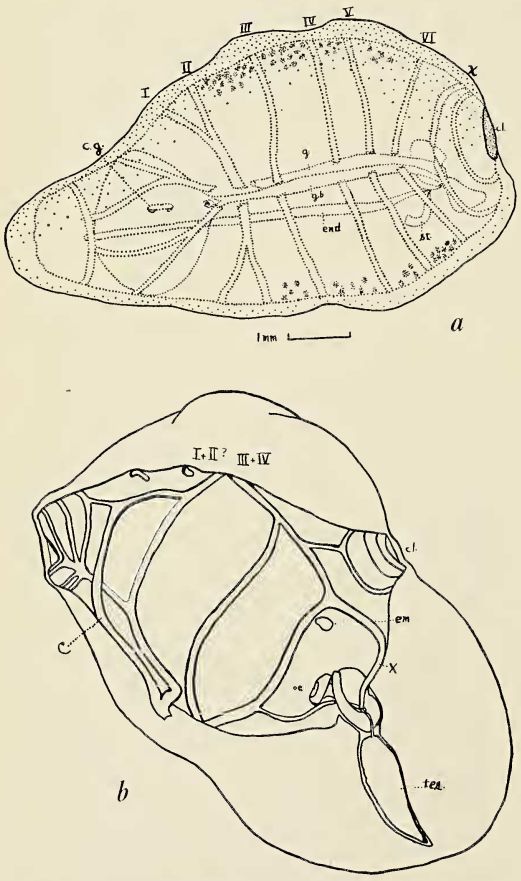


FIG. 5. *Cyclosalpa floridana. a*, Solitary form, dorsal surface; *b*, aggregate form, left side (modified after Metcalf, 1918).

Salpa (*Cyclosalpa*) *floridana* Metcalf, 1918: 32; Sewell, 1926: 72.
[non] *Cyclosalpa floridana* Apstein 1906*a:* 248; 1906*b:* 162.

SOLITARY FORM: One specimen examined with length of 8 mm. (Fig. 5*a*). *Test:* Rather thick, glutinous; with no definite elevations or depressions; rather far separated from mantle; attached at mouth and cloacal opening. *Muscles:* All six interrupted dorsally, ventrally continuous and fused into a single mass; M I–II joining dorsally; M I joining mouth muscles. *Ciliated groove:* Simple crescent with points turned ventrally. *Viscera:* Esophagus joins intestine ventrally at level of M VI; single, ventral caecum projecting from point where intestine courses antero-obliquely with gill; anus opening at level of M II (Metcalf shows this anterior to M I just under ganglion); light organs patchy masses of cells between the following muscles on each side: II–III–IV–V–VI.

AGGREGATE FORM: Two specimens examined, with lengths of 2.5 and 4 mm.

As both POFI specimens are in very poor condition, the following description is based on Metcalf, as is the figure (Fig. 5*b*). *Test:* Thin, far separated from body except at mouth and cloacal openings; forming a large bulge or swelling posteroventrally for testis and gut. *Muscles:* Three body muscles; M I joining mouth muscles and, with M C, forming peduncle muscles; M I–II and III–IV–x converging dorsally; M III–IV–x joining dorsally, converging ventrally; all muscles continuous dorsally and ventrally; x joining y by a bridle piece which extends over gut. *Ciliated groove:* Simple crescent. *Viscera:* Intestine forming a close loop, anus opening on left behind esophageal opening; testis large, projecting posteroventrally from gut; embryo located between M IV and x laterally.

Cyclosalpa bakeri Ritter (1905)
Fig. 6*a–c*

Cyclosalpa bakeri Ritter, 1905: 54; Ihle, 1935:

527–529; Thompson, 1948: 114; Tokioka, 1951: 183.

Cyclosalpa floridana Apstein, 1906*a:* 248; 1906*b:* 162.

[non] *Salpa floridana* Apstein, 1894*b:* 9.

Salpa (*Cyclosalpa*) *bakeri* Metcalf, 1918: 37.

SOLITARY FORM: One specimen examined with length of 34 mm. (Fig. 6*a*, *b*). *Test:* Thin, flabby, glutinous; closely attached to mantle; no definite elevations or depressions; pear-shaped with posterior end smallest. (This does not agree with the figure of Metcalf, which shows the test far separated from the mantle.) *Muscles:* Six body muscles, of which M I joins mouth muscles laterally and ventrally; all body muscles and x dorsally interrupted (Ritter, 1905, and Metcalf, 1918, say that x is sometimes complete dorsally), all except x ventrally interrupted (the above-named authors say that x is also ventrally interrupted); ventrally, y fusing with its fellow of the opposite side, extending shortly anteriorly between the gut caeca; dorsally M VI extending anteriorly almost to level of M II (to level of M IV according to Ritter and Metcalf); left and right anterior dorsal extensions of M VI remaining distinct. *Ciliated groove, ganglion and eye:* Ciliated groove forming an open U with left horn extended farther anteriorly; ganglion and eye just anterior to M I. *Viscera:* Esophagus opening at region of M VI ventrally; intestine accompanying gill antero-obliquely, anus opening behind eye level; two equally long, laterally compressed caeca projecting posteriorly; stolon held within a mantle tube which opens at level of M I–II; light organs large and distinct, four on one side, three on other in POFI specimen; each located laterally over a body muscle (previous reports show five large light organs and one small anterior one, between body muscles).

This animal most closely resembles the *polae* form of *Cyclosalpa pinnata* (according to the description of Sigl, 1912*a*, and the statement of Thompson, 1948). It can be distinguished from that form by the nonfusion of the two M VI dorsally, and by the fact that in *C. bakeri* the caeca are of equal length, whereas in *C. pinnata* they are unequal.

AGGREGATE FORM: Eight specimens examined with length range of 7–9 mm. (Fig. 6*c*). *Test:* No definite elevations or depressions; flabby, thin except around posterior projections; either closely applied or far separated from mantle; attached at cloacal siphon and mouth; two prominent posterior end projections of thicker test present; the whorl of zooids released from the stolon covered by an outer coat of test, including seven zooids both in my specimens and in Thompson's figure (1948, pl. 42). *Muscles:* Two main muscle groups dorsally; each dividing laterally into several branches; anterior group joining mouth muscles; peduncle muscles three on each side, anterior one from M C, lateral one from M I–II, and a short posterior one from M III which extends anteroventrally toward peduncle; muscles of posterior muscle mass continuous ventrally; muscle structure asymmetric. *Ciliated groove, ganglion and eye:* All anterior to M I; ciliated groove forming a crescent rather far anterior to ganglion and

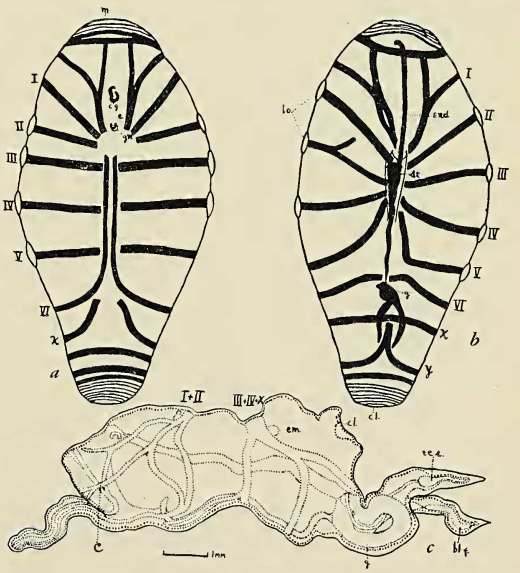


FIG. 6. *Cyclosalpa bakeri. a*, Solitary form, dorsal aspect; *b*, solitary form, ventral aspect (*a* and *b* schematic; length of animal, 34 mm.); *c*, aggregate form, left side.

eye; latter just in front of M I, prominent. *Viscera:* Gut forming posterior loop at base of posterior projections beyond body margin; anus opening at esophageal level; testis occupying left posterior projection; a caecum from the gut plus a smaller "problematic" organ, considered by Metcalf to be probably homologous with the same organ (=blood-forming organ) of *Ritteriella*, occupying the right posterior projection; embryo located at region of posterior muscle mass on right side.

Genus Helicosalpa Todaro, 1902

I have not seen the report of Todaro (1902) establishing this genus. Ihle (1935) stated in regard to Todaro's report, "Durch die starke Enantiomorphie, durch das Fehlen einer ringförmigen Anordnung der Blastozooide in der Kette und durch die eigentümlichen Haft-Flächen weicht *Cyclosalpa virgula* (Vogt) so bedeutend von den anderen Arten ab, dass Todaro (1902) diese Art zur selbständigen Gattung *Helicoslapa* rechnete." Ihle did not follow this classification, considering the species *C. virgula* to agree so closely with the other cyclosalpas in muscle arrangement and structure of gut that he thought it should not be separated from them.

After careful examination of the species *H. virgula* and *H. komaii*, however, I am of the opinion that they are quite different from the species of *Cyclosalpa;* thus I agree with Todaro (1902). As *Helicosalpa virgula* was at that time the only known species of the genus, it must be considered the type.

The genus may now be characterized as follows.

1. There are two distinct gregarious forms produced on the stolon, the dextral and the sinistral individuals. Whorls are not produced on the stolon. Mirror imagery is shown in the arrangement of attachment organs, musculature, tentacle over the ciliated groove, the ciliated groove, testis, and posterior projection (*H. virgula*), eye, mouth, and cloacal siphon. Other variations in the two forms, although not mirror imagery, are the position of the testis and posterior projection (*H. komaii*), embryo, gut, and anus ("primary asymmetry" of Komai, 1932; the mirror imagery is called "secondary asymmetry" by him). In a few other species of Salpidae (for example, *Brooksia rostrata* and *Ihlea punctata*) asymmetry occurs, but this apparently is secondary asymmetry.

2. There is no peduncle, only a blunt attachment organ by which the gregarious forms attach to the stolon. The body muscles do not enter this process as do the peduncle muscles of *Cyclosalpa*.

3. The solitary form possesses dorsal and ventral longitudinal muscles which are continuous with M I; the dorsal longitudinal muscles are paired (*H. virgula*) or united (*H. komaii*). The ventral longitudinal muscles are always paired; they are distinct from most transverse muscles (*H. virgula*) or joined by all transverse (body) muscles (*H. komaii*).

4. The anus of the solitary form is turned widely posteriorly from the anterodorsal region of the gill bar, forming a rectum.

The nearest known relative of *Helicosalpa virgula* and *H. komaii* is probably *Cyclosalpa bakeri*. Metcalf (1918) included *H. virgula* and *C. bakeri* in his group *Cyclosalpae asymmetricales* but did not attain a phylogenetically accurate division, stating: "The division of the subgenus into *Cyclosalpae symmetricales* and *Cyclosalpae asymmetricales*, while truly descriptive of the existing conditions, does not represent accurately degrees of relationship, for *Cyclosalpa bakeri*, an asymmetrical form, finds it nearest relative in *C. floridana*, an aberrant member of the group *symmetricales*."

The separation of *H. virgula* and *H. komaii* into a separate genus is considered phylogenetically valid, distinguishing them from the cyclosalpas.

Helicosalpa virgula (Vogt) 1854
Fig. 7*a–d*

Salpa virgula Vogt, 1854: 11.

Salpa dolicosoma Todaro, 1883: 41.
Salpa dolicosoma-virgula Traustedt, 1885: 360.
Helicosalpa virgula Todaro, 1902: 405.
Cyclosalpa virgula Apstein, 1906*b:* 161; Ihle, 1935: 527–529; Ihle and Ihle-Landenberg, 1936: 274; Thompson, 1948: 118.
Salpa (*Cyclosalpa*) *virgula* Streiff, 1908: 15; Metcalf, 1918: 43; Sewell, 1926: 73; Stiasny, 1926: 418.
[non] *Cyclosalpa dolicosoma-virgula* Traustedt, 1893.
[non] *Salpa* (*Cyclosalpa*) *virgula* Komai, 1932: 70.

SOLITARY FORM: One specimen examined with length of 141 mm. (Fig. 7*a*,*b*). *Test:* The test of this specimen is relatively huge compared with the body. Volumetric measurements were made by water displacement: the body measured 10 milliliters, whereas the test measured 148 milliliters. This great difference in volume has not been reported before, thus perhaps it is only an anomaly. Test globular, gelatinous, thick and flabby; slightly glutinous; formed of an outer thin membranous layer and a thick inner gelatinous layer; loosely attached to the body by a few fine strands of test tissue; without permanent elevations or ridges. Posterior languets shown by Metcalf (1918) not present in POFI specimen, but a pair of short test projections present at the cloacal region. *Muscles:* M I and VI are continuous dorsally on each side, forming two dorsal longitudinal muscles; M I extending posteriorly on ventral surface forming two ventral longitudinal muscles that end at region of stolon extrusion; M V interrupted dorsally, extending ventrally almost to stolon level as an anteriorly directed longitudinal muscle, thus almost meeting the posteriorly extended M I; M II, III, IV, and x dorsally and ventrally interrupted; M I joining mouth muscles. The close relationship of this species and *H. komaii* is evident from the similarity of muscle structure. It can easily be distinguished from it, as *H. virgula* possesses two dorsal longitudinal muscles rather than

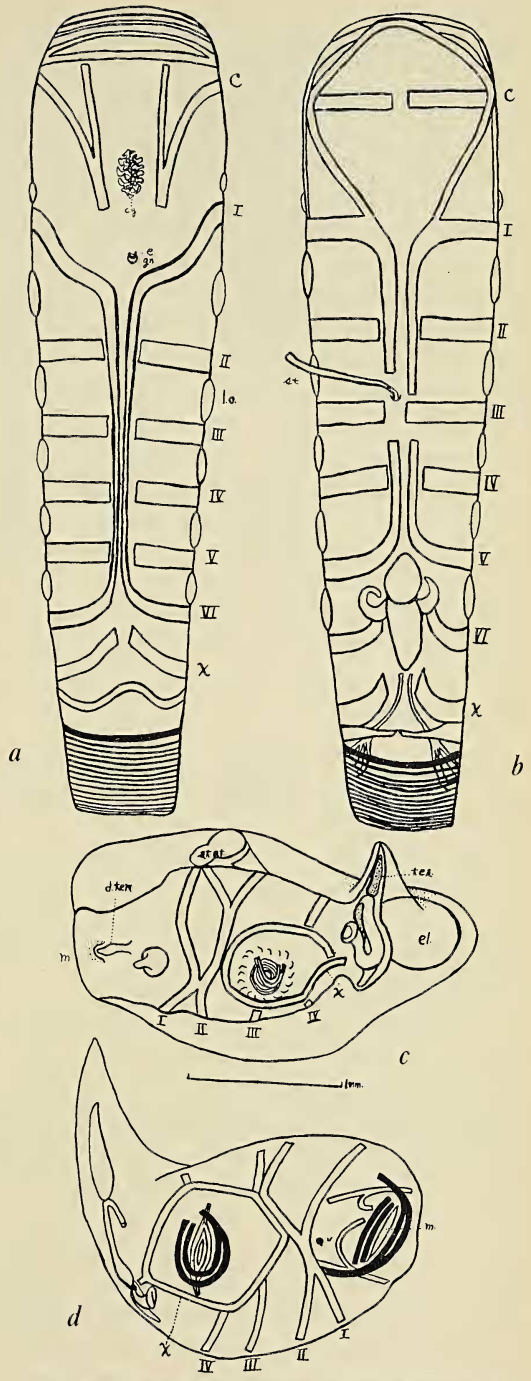


FIG. 7. *Helicosalpa virgula. a*, solitary form, dorsal aspect; *b*, solitary form, ventral aspect (*a* and *b* schematic, not showing the test; length, 141 mm.); *c*, aggregate form, sinistral individual from stolon, dorsal aspect; *d*, aggregate form, dextral individual, dorsal aspect (after Ihle, 1937–39, modified from Streiff, 1908).

one, and the ventral longitudinal muscles of *H. virgula* are not continuous (Streiff, 1908, however, represented them as continuous). In addition, the ventral ends of M II–IV remain distinct from longitudinal muscles in *H. virgula*. *Ciliated groove, ganglion and eye:* Ciliated groove highly convoluted, located at level of dorsoposterior extensions of M C; ganglion and eye at level of dorsal longitudinal muscles. *Viscera:* Gut large, bearing two caeca; intestine extending obliquely with gill, turning posteriorly at level of M I; stolon extruding from test at level of M III; six light organs on each side between body muscles from I to VI; additional small light organ anterior to M I (Streiff, 1908, Metcalf, 1918, and Stiasny, 1926, show a single continuous light organ extending from M I to M VI on each side; the photograph by Thompson, 1948, also shows a continuous light organ on each side; evidently, there is considerable variation in their location and structure).

AGGREGATE FORM: Only stolonic individuals were studied with length of 3 mm. (Figs. 7*c*,*d*).

The aggregate forms of this species and *Helicosalpa komaii* are the most asymmetric of all the salps. The two types of aggregate individuals that are produced, dextral and sinistral, are described separately.

Dextral individual (Fig. 7*d*): This has been figured by Streiff (1908) and Metcalf (1918). In addition, Streiff described the sinistral individual, but Metcalf apparently had only dextral individuals for study. Test thick and firm with a bulbous swelling around elaeoblast and a large pointed projection containing part of gut and testis projecting dorsolaterally toward anterior left side of body; anus directed toward right; eye turned slightly to right of mid-line of body, as is the cloacal opening; four body muscles; x prominent, encircling cloaca, separating the two parts of M IV; dorsal tentacle projecting over ciliated groove to left of and anterior to ganglion.

Sinistral individual (Fig. 7*c*): Test similar to above, except projection containing gut and testis directed to right; anus directed toward left; ganglion and eye slightly to left of mid-line of body, as is cloacal opening; muscles the mirror image of dextral individual; dorsal tentacle over ciliated groove projecting anteriorly and slightly to right of ganglion.

Helicosalpa komaii
(Ihle and Ihle-Landenberg) 1936
Fig. 8*a–f*

Salpa (*Cyclosalpa*) *virgula* Komai, 1932: 70.
[non] *Salpa virgula* Vogt, 1854: 11.
Cyclosalpa komaii Ihle and Ihle-Landenberg, 1936: 274; 1938*b*: 609; Tokioka, 1937: 221.
Cyclosalpa virgula Fedele, 1937: 448, 525 (*fide* Ihle and Ihle-Landenberg, 1938*b*).
[non] *Salpa virgula* Vogt, 1854: 11.

SOLITARY FORM: One specimen examined with length of 94 mm. (Komai's specimen was 230 mm. long, making this the largest of all known salps.) (Fig. 8*a–d*.) *Test:* Thick, flabby, strongly attached to mantle by numerous fine strands of test material; a prominent, nonserrated, middorsal ridge present on anterior half of test; without other permanent elevations or depressions; test composed of a thin outer layer and a thicker inner gelatinous layer; inner layer opaque (staining makes it more opaque, so should be used only with caution). Komai (1932) stated, "The test is thin and soft." I presume that he examined only the outer surface, which appears without dissection to be thin and rather far separated from the mantle by the inner gelatinous layer. *Muscles:* Six body muscles; x and y branched (Komai's figure, 8*c* of this report, shows y as a nonbranched muscle); mouth musculature including the large M C that approaches or touches M I dorsolaterally, passes backward ventrally as the ventral longitudinal muscle; two large sphincters of the dorsal lip (according to Komai, one large posterior and three small anterior ones) appearing to fuse laterally with two sphincters of the ventral lip, then continuing posteriorly as a dorsal retractor to the outside

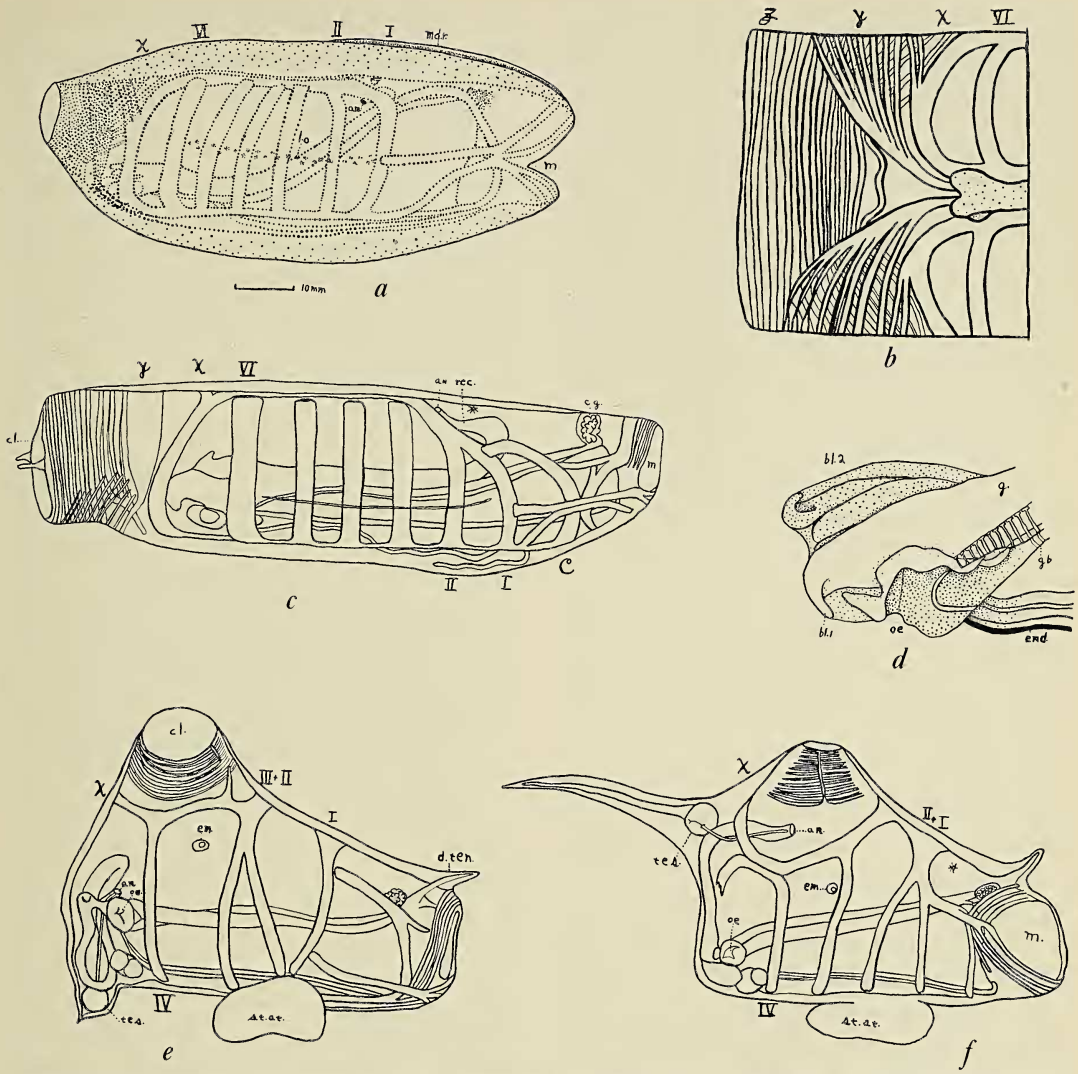


FIG. 8. *Helicosalpa komaii. a*, Solitary form, right side; *b*, solitary form, inside view of ventral cloacal region; *c*, solitary form (230 mm.), right side (after Komai, 1932); *d*, solitary form, posterior part of gut, right side (blind sac 2 has been turned slightly dorsad); *e*, aggregate form (about 50 mm.), sinistral individual, right side; *f*, aggregate form (about 70 mm.), dextral individual, right side. (*e* and *f* after Komai, 1932).

of M I, and as a ventral retractor which courses with M C as part of the ventral longitudinal muscle. Komai shows the dorsal retractor muscle formed only by ventral lip sphincters 1 and 2, the ventral retractor muscle formed by ventral lip sphincter 3. The specimen before me is rather mutilated anteriorly, so my description perhaps is wrong in some details. M I–II continuing dorsally as unpaired dorsal longitudinal muscle joining x; x forming ventral longitudinal muscle (paired) which receives contributions from all body muscles as well as ventral retractor and M C of mouth region; there is thus a continuous rectangular muscle band which includes parts of all the major muscles of this animal. *Ciliated groove, ganglion and eye:* Ciliated groove highly convoluted, located anteriorly at level of M C; ganglion and eye at level of M I–II, just over rectum. *Viscera:*

Intestine elongate, coursing obliquely dorsad with gill, separating from it at level of M I forming a prominent posterior bend (rectum); forming two prominent caeca posteriorly which project equally posteroventrally in the POFI specimen, whereas Komai's figure shows one caecum projecting dorsoanteriorly, the other posteroventrally; stolon passing anteriorly in sinuous course, turning posteriorly just in front of M I (from Komai; the POFI specimen has no stolon); light organ composed of sparse masses of cells from M I–VI on each side of body.

AGGREGATE FORM: As no specimens of this form have been examined, the description follows those of Komai (1932) and Tokioka (1937). Length range of known specimens (Komai) 20–55 mm. without projections.

Dextral individual (Fig. 8*f*): Body ovoid, texture soft; one long posterior projection present; a cushion-shaped attachment organ on left ventral surface; atrial opening dorsal, tubular; musculature closely similar to that of *H. virgula;* gut forming open U-shaped loop at base of posterior projection; esophagus and left ventral caecum directed anteriorly; intestine extending dorsally, rectum bending anteriorly; small right caecum protruding to the right; testis spherical, located posterior to gut at base of posterior projection; a "whitish core" extending from testis to rear of posterior projection (considered by Komai probably homologous to the blood-forming organ of *Ritteriella*); ciliated groove highly convoluted; a prominent horn-like process borne dorsoanteriorly over ciliated groove.

Sinistral individual (Fig. 8*e*): Musculature the mirror image of that of dextral individual; attachment organ on right ventral surface; horn-like projection over ciliated groove extending dorsally toward right; posterior projection short, forming a blunt cone; esophagus and anus close to one another, located dorsally; esophagus coursing posteriorly, intestine bending ventrally, then dorsally and opening on left side of esophagus; left caecum large, opening into upper part of intestine of left; right caecum small, opening below left one on right side; testis spherical, ventral to gut, in base of cone-shaped projection.

Embryo in both types located on dorsal right side between M III and IV. The horn-like projection is absent in very young individuals (as this is present in young *H. virgula* from the stolon, perhaps this is incorrect).

This species has been reported only from Seto, Japan (Komai, 1932), and the present specimen is from 7°4′′N, 140°4′′W. Komai (1932) described both the solitary and aggregate forms (one and *ca.* 30 specimens, respectively), considering them *S.* (*C.*) *virgula.* Ihle and Ihle-Landenberg (1936) studied *H. virgula* critically, comparing their observations with those of Komai. They concluded that his specimens were a distinct species which they named after him. Tokioka (1937) agreed with this conclusion and figured and described the gut and associated structures of gregarious specimens, apparently from the same collection on which Komai worked.

Fedele (1937) found that the dorsal tentacle above the ciliated groove of gregarious individuals is also present in *H. virgula.* He considered the spherical testis of *H. komaii* to be only a condition of age and therefore regarded Komai's specimens as identical with *H. virgula.* Ihle and Ihle-Landenberg (1938*b*) wrote a short note defending their earlier conclusion. They agreed that the dorsal tentacle is also found in *H. virgula,* but the spherical testis was not present; this conclusion is supported in the present report, as all stolonic individuals of *H. virgula* possess an elongate testis, never a spherical one. In addition, the solitary form of *H. komaii* is so different from *H. virgula* that they regarded their earlier conclusion as the correct one, with which I am in complete agreement.

SALPINAE subfam. nov.

This subfamily may be distinguished by the following characteristics: (1) In both forms the gut is completely free from the gill, except at the esophageal region, and does

not accompany the gill; (2) there are no distinct light organs present in either form (the gut of some species produces light from diffuse bodies); (3) the gut in the aggregate form is a more or less compact "nucleus," never a loosely formed loop or an extended tube; (4) attachment organs in the aggregate form are separated, not united into one process; thus, there are two or more attachment organs in each animal.

Genus BROOKSIA Metcalf, 1918

Solitary form with six body muscles, aggregate form with four and five. Solitary form with an anterior snout containing two pairs of longitudinal muscles, the dorsal pair continuous with the mouth musculature, the ventral pair formed by M I and C?. Ventral longitudinal muscles extend posteriorly to gut region. Aggregate form with testis outside intestinal coil, with short anteriorly upturned endostyle. Aggregate form asymmetric.

One species, *Brooksia rostrata*.

Brooksia rostrata (Traustedt) 1893

Fig. 9*a–e*

Salpa rostrata Traustedt, 1893: 8; Sigl, 1912*b* (*fide* Thompson, 1948).

Salpa (*Brooksia*) *rostrata* Metcalf, 1918: 50; Sewell, 1926: 84.

Brooksia rostrata Ihle, 1935: 527–529; Ihle and Ihle-Landenberg, 1935: 24; Thompson, 1948: 120.

SOLITARY FORM: More than 10 specimens examined, with length range of 2–31 mm. without snout (probable range of 4–62 mm. with snout). (Fig. 9*b–e*.) *Test:* Flabby, glutinous, without permanent elevations or depressions; usually absent or fragmentary in preserved specimens. *Muscles:* Six dorsally continuous body muscles present; M I–III and IV–V–VI–x forming groups dorsally; M III–IV touching laterally; a strong longitudinal muscle coursing on each side of endostyle from gut to anterior tip of snout (they remain separate throughout their length); these longitudinal muscles joined by M C? and M I only (this is contrary to Traustedt, 1893, and Thompson, 1948, but on close examination, one can see that no other muscle fuses with them as Ihle, 1910, showed). In addition to extensions of the ventral longitudinal muscles, the snout contains two dorsal longitudinal muscles that continue with the oral retractor. I have thus classified them as M b_3, or ventral lip sphincter 3. The oral retractor is formed by the first dorsal lip sphincter (A_1) and all three ventral lip sphincters. M B_1 and C extend to just behind the oral retractor. An independent muscle, probably formed from M C or B_1 (I have labeled it C?), extends ventrally to join the ventral longitudinal muscle, as does M I. In one specimen, M I is dorsally interrupted, probably unnaturally. The horizontal muscle (*c*) is long and relatively narrow. The cloacal musculature of Figure 9*c*, *d* has been reconstructed from fragments. *Ciliated groove, ganglion and eye:* Ciliated groove long, sinuous in large specimens, short and simple in smaller ones. The eye has the usual horseshoe shape. Ganglion and eye lateral to ciliated groove in large specimens, dorsal to it in smaller ones. *Viscera:* Gut somewhat compressed laterally; margined by a thin flap of caecum (?) tissue; in state E (Ihle and Ihle-Landenberg, 1935). The stolon is directed posteriorly.

AGGREGATE FORM: More than 10 specimens examined with length range of 0.8–2.5 mm. (Fig. 9*a*). *Test:* Flabby, glutinous, usually absent in preserved animals. *Muscles:* Body muscles fused dorsally and ventrally into a single mass; asymmetric, with two types produced, the sinistral and dextral individual, whose muscles are mirror images. There are apparently four body muscles on one side and five on the other, but due to the invariably poor condition of preserved specimens, musculature is difficult to study; consequently, this needs further examination. *Ciliated groove:* Simple, anterior to M I. *Viscera:* Anterior end of endostyle widely turned dorsally; endostyle short; gut in state A (Ihle, 1937–39);

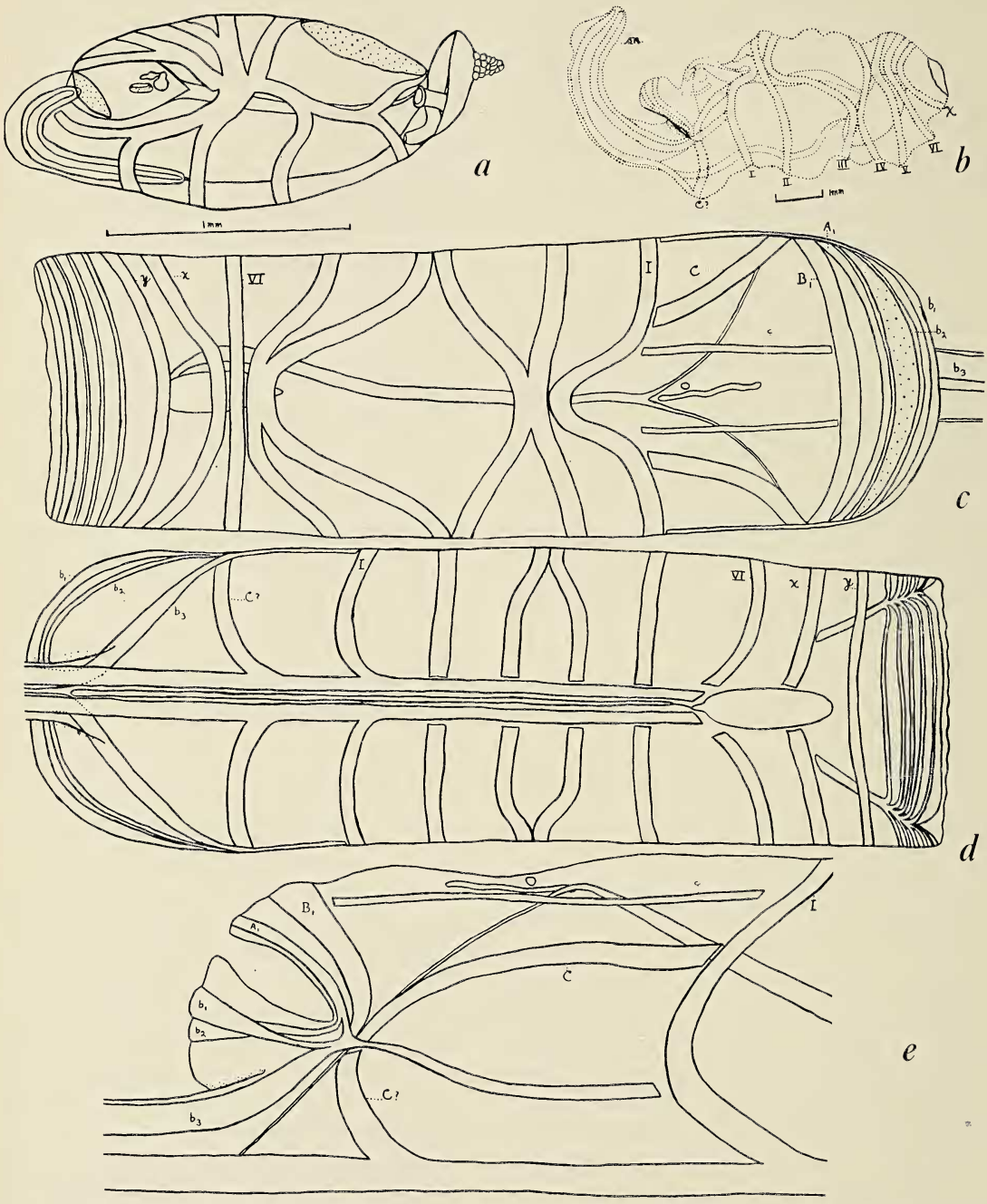


FIG. 9. *Brooksia rostrata*. *a*, Aggregate form, left dorsal aspect; *b*, solitary form, specimen without test, left dorsal aspect; *c*, solitary form, diagram of dorsal surface (length without snout, 31 mm.); *d*, same specimen as *c*, ventral surface; *e*, same specimen as *c*, mouth region, left lateral aspect.

testis located posterior to gut, unlike all other Salpinae.

This form, because of its small size, is easily confused with *Thalia democratica* agg. The presence of the widely turned endostyle, prominent gut with posterior testis, and dorsal and ventral muscle masses make it readily distinguishable.

Previously this species has been considered rare, although, as Apstein (1894) and Thompson (1948) stated, the very small aggregate form may easily be overlooked, especially among large numbers of *Thalia democratica* agg. The species is common in the POFI collections; in one plankton sample, for example, there were 8 solitary and 38 aggregate zooids. These animals are delicate and usually fragmented. Only two specimens of the solitary form retained the snout. The solitary zooid can be positively identified by the longitudinal muscles coursing parallel to the endostyle; the aggregate zooids must be examined closely, preferably stained, for correct identification. Fragments should not be overlooked but stained and examined, as the snout is useful as a recognition character only if the animal is whole. The high muscular activity of the solitary zooid was shown by the fact that in many specimens the body was turned completely inside out.

Genus IHLEA Metcalf, 1919

Solitary form with six or seven body muscles which form complete rings. Aggregate form with five or six body muscles which form complete rings or are ventrally interrupted; these muscles are arranged asymmetrically.

Two species, *Ihlea punctata* (type) and *I. magalhanica*. The latter species has not been found in the POFI collections.

Ihlea punctata (Forskål) 1775
Fig. 10*a–c*

Salpa punctata Forskål, 1775: 114; Ihle, 1912: 34.
Biphora punctata Bruguière, 1789: 181.
Salpa musculosa [?] Herdman, 1888: 64.
Salpa musculosa-punctata Traustedt, 1893: 6.
Salpa asymmetrica Fowler, 1896: 994; Ihle, 1912: 35.
Salpa (Salpa) punctata Streiff, 1908: 25.
Salpa (Apsteinia) punctata Metcalf, 1918: 72 (see also Metcalf, 1919).
Salpa (Apsteinia) asymmetrica Metcalf, 1918: 78, 183 (see also Metcalf, 1919).
Ihlea punctata Ihle, 1935: 527–529.
Ihlea asymmetrica Ihle, 1935: 527–529; Tokioka, 1937: 222; Berrill, 1950: 300.

SOLITARY FORM: Eight specimens examined, with length range of 3 (embryo)–14 mm. (Fig. 10*a*). *Test:* No specimen of the solitary and aggregate generations except the embryo had the test attached. It is probably loosely attached to the adult. The test of the embryo is flabby, rather thick around gut and elaeoblast area; without distinct elevations or de-

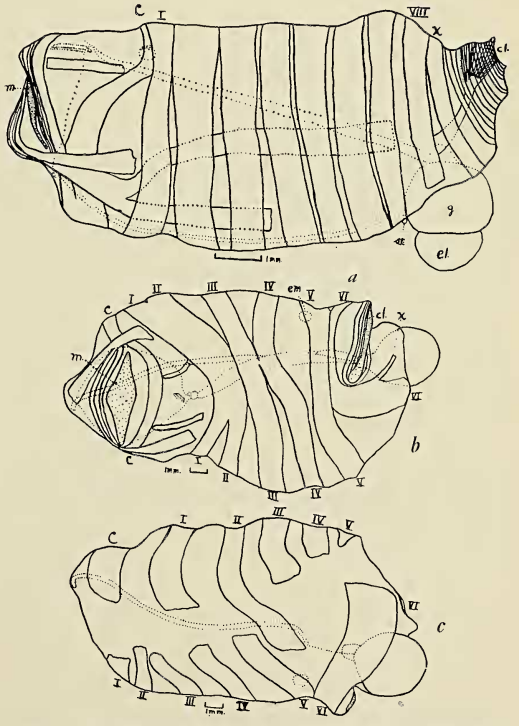


FIG. 10. *Ihlea punctata*. *a*, Solitary form, left side, slightly dorsal; *b*, aggregate form, dorsal aspect; *c*, aggregate form, ventral aspect.

pressions; with one lateral attachment organ on each side over cloacal muscle x. *Muscles:* Ten large muscles of which the first is M C; M I fused with C dorsally; M VI–VII fused ventrally; remaining body muscles distinct dorsally and ventrally; M C, I–VII, and x forming complete rings; M VIII interrupted ventrally, continuous dorsally; ventral oral retractor extending posteriorly on each side, branching into two longitudinal bands, a dorsal one extending to posterior edge of M VII and a ventral one extending to space between M III and IV (touching IV in embryo); longitudinal muscles coursing internally to body muscles; cloacal retractor extending anteriorly beneath x to M VIII. *Ciliated groove, ganglion and eye:* Ciliated groove simple, anterior to M C. Ganglion and eye just beneath M C. *Viscera:* Gut compact, in condition D (Ihle and Ihle-Landenberg, 1933); stolon, according to earlier investigators, forming a tight spiral limited to ventral region of gut (no stolon present in POFI specimens).

AGGREGATE FORM: More than 10 specimens examined with length range of 18–23 mm. (Fig. 10*b,c*). *Test:* Not observed but body flabby, thus test probably without permanent elevations or depressions. *Muscles:* Asymmetric; six body muscles present; M I–II join dorsally as do III–IV and V–VI; all muscles interrupted ventrally; M C broad; M VI on one side extending in broad band around ventral surface of gut; M II on side opposite latter portion of VI extending posteriorly on ventral surface toward opposite side to between M V and VI. *Ciliated groove, ganglion and eye:* All anterior to M I; ciliated groove straight, simple; ganglion and eye posterodorsal to it; eye projecting dorsally toward a small opening in mantle above it. *Viscera:* Gut compact, in condition F (Ihle and Ihle-Landenberg, 1933); embryo located on right side just under M V.

On examination of the literature of *Ihlea punctata* and *I. asymmetrica*, a large number of contradictions, seemingly incorrect observations, and similarities in the descriptions of the two so-called species are noticeable.

Therefore, if some of the earlier works which seem to be permeated with faulty observations are disregarded, the reported differences between the species and my criticisms of them may be summarized as follows:

1. In *Ihlea asymmetrica* aggregate there are no pigment cells ventrally on the test, whereas in *I. punctata* these are present. The presence or absence of pigment is probably largely determined by length of exposure to the preservation fluid.

2. In *I. asymmetrica* agg. all body muscles are interrupted ventrally (Ihle, 1912; Tokioka, 1937) or only M VI is a ring (Metcalf, 1918), whereas in *I. punctata* all muscles are interrupted ventrally (Streiff, 1908; Ihle, 1912; Metcalf, 1918). Metcalf (1918) performed his study on stolonic individuals of *I. asymmetrica* which perhaps had not completed their growth and thus possessed a ring muscle; or he made an error in his observation.

3. In *I. asymmetrica* agg., M I–II and V–VI join dorsally to form groups, M III and IV remain separate (Metcalf, 1918), or M I–II, III–IV, and V–VI form groups, the second group (III–IV) joining the first (Ihle, 1912; Tokioka, 1937). On the other hand, *I. punctata* forms two groups—M I–II and V–VI—and M III–IV remain separate (Streiff, 1908; Metcalf, 1918), or M I–II and V–VI form groups, M II–III remain separate but approach M II (Traustedt, 1893; Apstein, 1906*a*). These differences in muscle grouping seem to be only individual variation. They overlap in part and are considered nonuseful here.

4. In *Ihlea asymmetrica* sol., the dorsal longitudinal muscle extends to M VIII; the ventral longitudinal muscle extends to beneath M V (Ihle, 1912; Metcalf, 1918). In *I. punctata*, on the other hand, the dorsal longitudinal muscle extends to between M VII and VIII (Apstein, 1906*a;* Streiff, 1908; Ihle, 1912; Metcalf, 1918); the ventral longitudinal muscle extends to between M III–IV (Apstein, 1906*a;* Streiff, 1908; Ihle, 1912; Metcalf, 1918). There is obviously no difference

in the dorsal longitudinal muscle extension. The difference described in the ventral extension is perhaps only one of growth. At any rate, it is rather minor.

5. In *Ihlea asymmetrica* sol. there are lateral projections on either side of the gut in embryos (and the small specimen of Ihle, 1912), whereas these have not been reported in *I. punctata* (Apstein, 1901, Ihle, 1912, and Metcalf, 1918, have reported them in *I. asymmetrica*). As Metcalf (1918) pointed out on his embryo, lateral projections are probably only embryonic attachment organs. Thus they may disappear in adults. They are presumably present in embryos of both so-called species.

6. In *I. punctata* sol. there are pigmented areas on the lips and posteroventral region near the gut (Metcalf, 1918), whereas these have not been reported in *I. asymmetrica*. Again, the presence or absence of pigment is probably largely determined by the length of exposure to preservation fluid.

7. In *I. asymmetrica* sol., the bow muscle (C) and I, II, III, and IV form one group dorsally, M VII, VIII, and x form another (Metcalf, 1918); or C–I–II form one group, III–IV form another, and M VIII and x form a third group (Apstein, 1901); or C–I–II form one group dorsally, M III–IV a second, and M VII–VIII–x form a third group (Ihle, 1912). On the other hand, in *I. punctata* C–I–II form the only group (Traustedt, 1893); or all remain separate (Apstein, 1906*a*,*b*; Streiff, 1908); or C–I–II form one group, and VII (?)–VIII–x (figures of Metcalf, 1918) form another. These differences in muscle grouping are probably only individual variation and are considered nonuseful here.

As a result of an exhaustive review of the literature, I can conclude only three possibilities: (1) the two species may be distinct, but, if so, the descriptions are in such a tangle that they are in large part unreliable; (2) the two so-called species are one, the differences described being due only to individual variation, not to specific, subspecific, varietal, or formal variation; (3) the two species are one, the differences described being due to variations important enough, perhaps, to consider *I. asymmetrica* to be only a form or variety of the main species, *I. punctata*. This form would be distinguished from the main species only by the length of the ventral longitudinal muscle and the absence of pigmented areas in the test.

It is my opinion that possibility 2, above, is the correct one. Therefore, the two species are here regarded as only one, *Ihlea punctata* (= *I. asymmetrica*), with no differences other than what can be attributed to individual variation.

This conclusion is upheld by an embryo (solitary form) in the POFI collections. This embryo's ventral longitudinal muscle extends up to the anterior edge of M IV (a character of *I. punctata*, presumably); it also, however, possesses attachment organs—one on each side over M x (a character of *I. asymmetrica*, presumably).

Genus SALPA Forskål, 1775

Solitary form with eight ventrally interrupted body muscles, aggregate form with six. In the aggregate form, these muscles form two groups dorsally. Transverse ridges of gill bar taper gradually to a point ventrally and are separated from one another by a distance less than 0.5 the width of the gill bar.

Two species, *Salpa maxima* (type) and *S. fusiformis*.

Salpa fusiformis Cuvier, 1804

Figs. 11*a–h*, 12*a–e*, 15*b*, 16*b*

Salpa fusiformis Cuvier, 1804: 382; Bomford, 1913: 243; Ihle, 1935: 527–529; Tokioka, 1937: 223; Thompson, 1948: 156; Berrill, 1950: 293.
Salpa aspera Chamisso, 1819: 14.
Salpa runcinata Chamisso, 1819: 16.
Biphora depressa Sars, 1829: 51.
Biphora tricuspidata Sars, 1829: 56.
Salpa clostra Deshayes, 1836–46: vol. 121, figs. 2–2a.

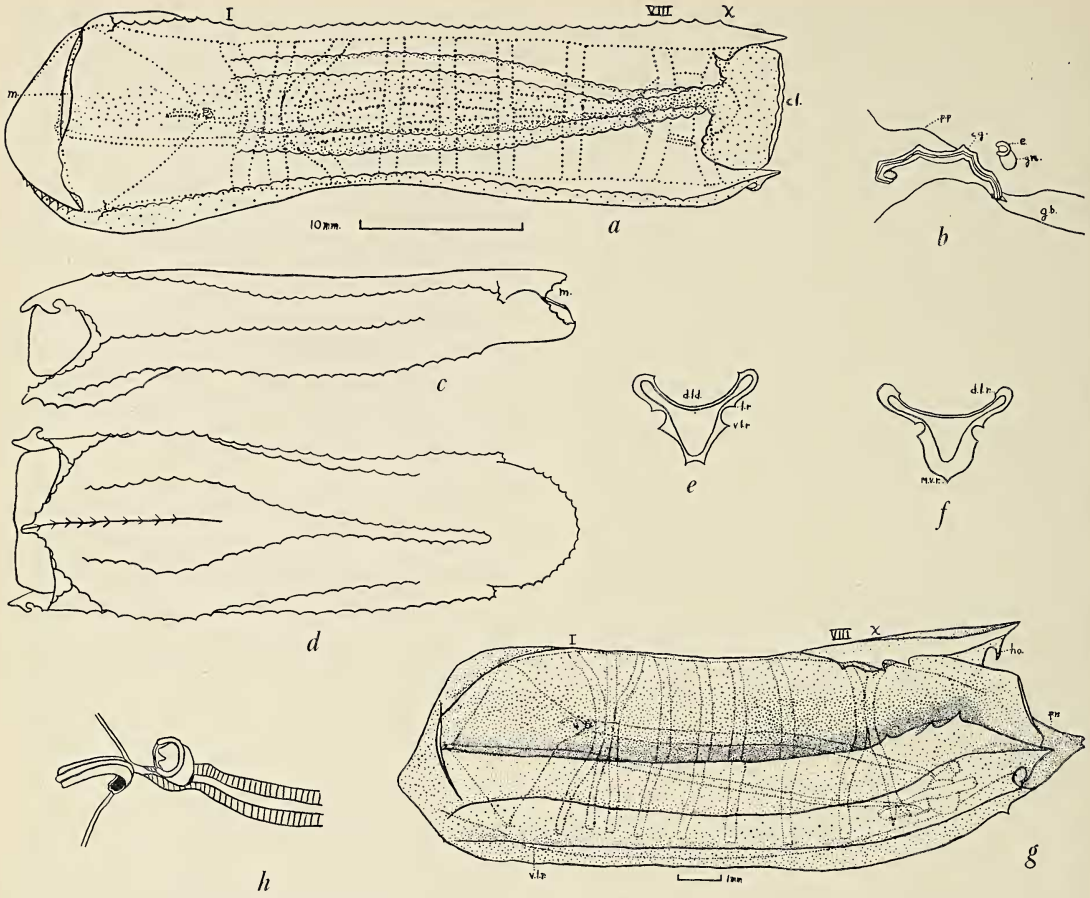


FIG. 11. *Salpa fusiformis*, solitary form. *a*, Asperate form, dorsal aspect; *b*, same specimen as *a*, ciliated groove and associated structures, dorsal aspect; *c*, same specimen as *a*, test, right side; *d*, same specimen as *a*, test, ventral surface; *e*, nonspiny form, scheme of cross section of test at level of M III; *f*, nonspiny form, scheme of cross section of test at gut level; *g*, nonspiny form, left dorsolateral aspect; *h*, same specimen as *g*, ciliated groove and associated structures, dorsal aspect.

Salpa runcinata-fusiformis Traustedt, 1885: 370.
Salpa echinata Herdman, 1888: 66.
Salpa runcinata-fusiformis var. *echinata* Apstein, 1894*a:* 47.
Salpa fusiformis var. *echinata* Apstein, 1894*b:* 14.
Salpa fusiformis-runcinata Ritter, 1905: 64.
Salpa fusiformis-runcinata form *echinata* Ritter, 1905: 67.
Salpa (*Salpa*) *fusiformis* Streiff, 1908: 24; Metcalf, 1918: 88; Sewell, 1926: 75; Stiasny, 1926: 424.
Salpa fusiformis forma *aspera* Ihle, 1911: 587; Tokioka, 1937: 223; Thompson, 1948: 158.
Salpa fusiformis fusiformis Ihle, 1912: 39.
Salpa fusiformis aspera Ihle, 1912: 40.
Salpa (*Salpa*) *fusiformis* form *aspera* Metcalf, 1918: 92; Sewell, 1926: 76.

SOLITARY FORM: More than 10 specimens examined with length range of 11–47 mm. (Fig. 11). *Test:* The typical form is described first (Fig. 11*g*): dorsal longitudinal depression wide and deep, limited on each side by a dorsal limiting ridge; each dorsal limiting ridge bearing posteriorly several spines, continuing into a dorsal posterior projection; test of dorsal longitudinal depression thin,

continuous with thin test of cloacal siphon; dorsal posterior projections bearing a blunt, straight, posterior spine and a curved ventral hook; each projection also forming a ventrally directed posterior ridge that joins the same ridge of opposite side midventrally; at joint, ventral posterior projection formed; each dorsal posterior projection bearing laterally an anteriorly directed lateral ridge; ventral to this, formed at the posterior ridge, a ventrolateral ridge courses anteriorly; ventrally a midventral ridge continuing anteriorly, dividing into two that continue to the chin; chin and mouth covered by thin test; internally test with rather large gut cavity, no elaeoblast cavity; cavity for posterior ventral attachment organ not present in typical specimens (may be present in large asperate specimens); margin of gut cavity smooth. The asperate form of this species is similar to the typical form, except that its ridges are spiny and the test has more thin area, being thick only posteriorly, at the chin and upper lip, and along ridges (Fig. 11*a*). *Muscles:* Eight body muscles; M I–III and VIII–x usually fuse, touch, or converge but may be separated; no attachment organ between M VI–VII. *Ciliated groove:* Usually forming shallow open bend (Fig. 11*b*) but may form a large structure resembling that of *Salpa maxima* (Fig. 11*b*). *Viscera:* Gut compact, in condition E (Ihle and Ihle-Landenberg, 1933); endostyle straight; stolon usually coursing anteriorly, turning abruptly and coursing around left side of gut, but may form a tight circle around gut.

AGGREGATE FORM: More than 10 specimens examined with length range of 5–37 mm. (Fig. 12). *Test:* In typical form (Fig. 12*a*), keg-shaped, smooth; with one anterior and one posterior end projection; each may be as long as body; dorsal longitudinal depression extending onto end projections, limited laterally by dorsal limiting elevations; ventrally test gradually raised, forming a relatively small gut swelling. There is an asperate form (Fig.

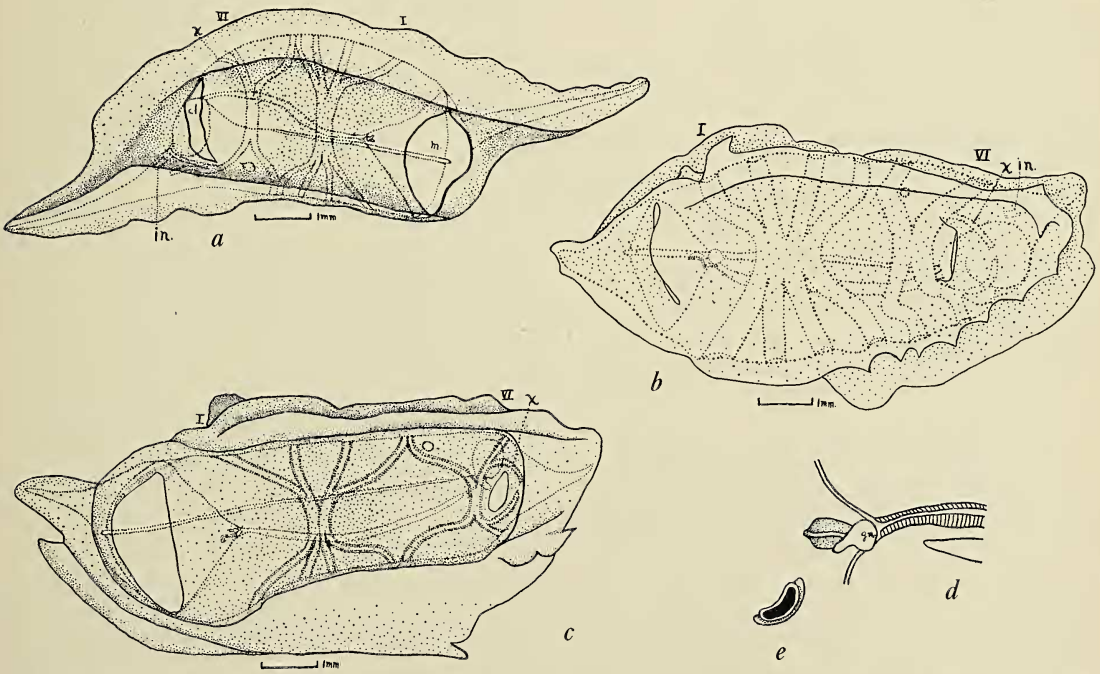


FIG. 12. *Salpa fusiformis.* aggregate form. *a*, Nonspiny form, dorsal aspect; *b*, asperate form, dorsal aspect; *c*, another asperate specimen, dorsal aspect; *d*, same specimen as *b*, dorsal aspect of ciliated groove and associated structures; *e*, ventral aspect of ciliated groove, from *d*.

12*b*,*c*) whose test is sparsely spined, asymmetric; end projections short, although Metcalf (1918) found some with long projections; test relatively thick. This form has broad muscle bands. *Muscles:* Six body muscles; M I–II and III–IV fusing dorsally as do M V–VI, thus forming two groups; M IV and V usually approach, touching or joining laterally, but as Stiasny (1926) pointed out, this is not so in many specimens; ends of muscles extending rather far ventrally. Ventral lip sphincter 4 (M b_3) interrupted. *Ciliated groove* (Fig. 12*d*, *e*): Simple, straight or slightly curved. *Viscera:* Gut compact, in condition C (Ihle and Ihle-Landenberg, 1933); gill segments closely approximated; embryo attached to right side dorsally behind or beneath M V.

Salpa maxima Forskål, 1775

Figs. 13*a–l*, 14*a–e*, 15*a*, 16*a*

Salpa maxima Forskål, 1775: 112; Ihle, 1935: 527–529; Tokioka, 1937: 223; Thompson, 1948: 154.
Salpa africana Forskål, 1775: 116.
Biphora maxima Brugiuère, 1789: 179.
Biphora africana Brugiuère, 1789: 182.
Salpa birostratus Blainville, 1827: 119.
Salpa chamissonis Lesson, 1830: 274.
Salpa forskalii [?] Lesson, 1830: 276.
Salpa birostrata Meyen, 1832: 412.
Salpa antarctica Meyen, 1832: 416.
Salpa naepolitana [?] Chiaje, 1841: 40.
Salpa africana-maxima Traustedt, 1885: 374.
Salpa (*Salpa*) *maxima* Streiff, 1908: 21; Metcalf, 1918: 83; Sewell, 1926: 83; Stiasny, 1926: 419.

SOLITARY FORM: Ten specimens examined with length range of 6 (embryo)–108 mm. (Fig. 13). *Test:* In typical specimen (Fig. 13*e*) thick in all areas, especially around gut; dorsal depression rather deep; two large dorsal limiting elevations; ventrolateral depression deep, gradually forming ventral elevation; spinose posteriorly; internally, test with large gut cavity whose posterior margin may bear elevations (called "baumförmigen Fortsätzen" of the cloacal tube, and therefore presumably of epithelium, by Streiff, 1908, and Ihle, 1912, and figured as such by them as well as later investigators); these internal test elevations may be absent or present, usually bearing several blunt spines which themselves may bear minute spines; a cavity projects ventroanteriorly from the gut cavity, housing the elaeoblast and reduced in older individuals that have resorbed the elaeoblast; anterior to gut cavity, a placental cavity present in smaller specimens; posterior to gut cavity a deep invagination for posteroventral attachment organ usually present; in one specimen (Fig. 13*e*), whole ventral region forming a cavity continuous with an opening in chin which appears to be natural, as its margin is not jagged, but not present in smaller specimens; chin prominent. In addition to the typical form, there is an echinate form that resembles the echinate form of *Salpa fusiformis* (Fig. 13*a*). It can be distinguished from the typical form only on the basis of the test. It should, perhaps, be described as typical, as this is the only form of the smaller specimens of *S. maxima* found here. Test has distinct thick and thin regions; thin dorsally and laterally except in posterior quarter of body; spines usually limited to posterior quarter of body (but not necessarily; see Fig. 13*l*); a deep longitudinal depression limited by dorsal limiting elevations (these may be ridges); transverse depression at base of upper lip; dorsal limiting elevations becoming thickened posteriorly, bearing a row of spines; just below this, a narrow longitudinal extension of thin test joins cloacal test; ventral to this a thickened region continuous posteriorly and ventrally from one side to opposite side; two weak ridges of spines on lateral surface of this thickened region; a group of spines on ventrolateral and ventral gut region; entire posteroventral region forming a gut swelling; ventral surface thickened along its entire length forming a large nonridged (but may be echinate) ventral elevation; chin rather prominent. The test as well as other structures

of *Salpa fusiformis* and *S. maxima* are in some specimens almost identical. Figure 13*l* shows a specimen of *S. maxima* of this type. *Muscles:* Eight body muscles, usually far separated from one another, but groups may be formed; extending only a short distance ventrally; attachment organ on each side dorsally between M VI and VII that may be prominent, reduced, or absent (Fig. 13*b*,*f*). *Ciliated groove* (Fig. 13*g*,*h*): Forms a large incomplete loop with three bends; in larger specimens, minor bends give the appearance of segmentation. *Viscera:* Gut compact, in condition F (Ihle and Ihle-Landenberg, 1933); stolon extending

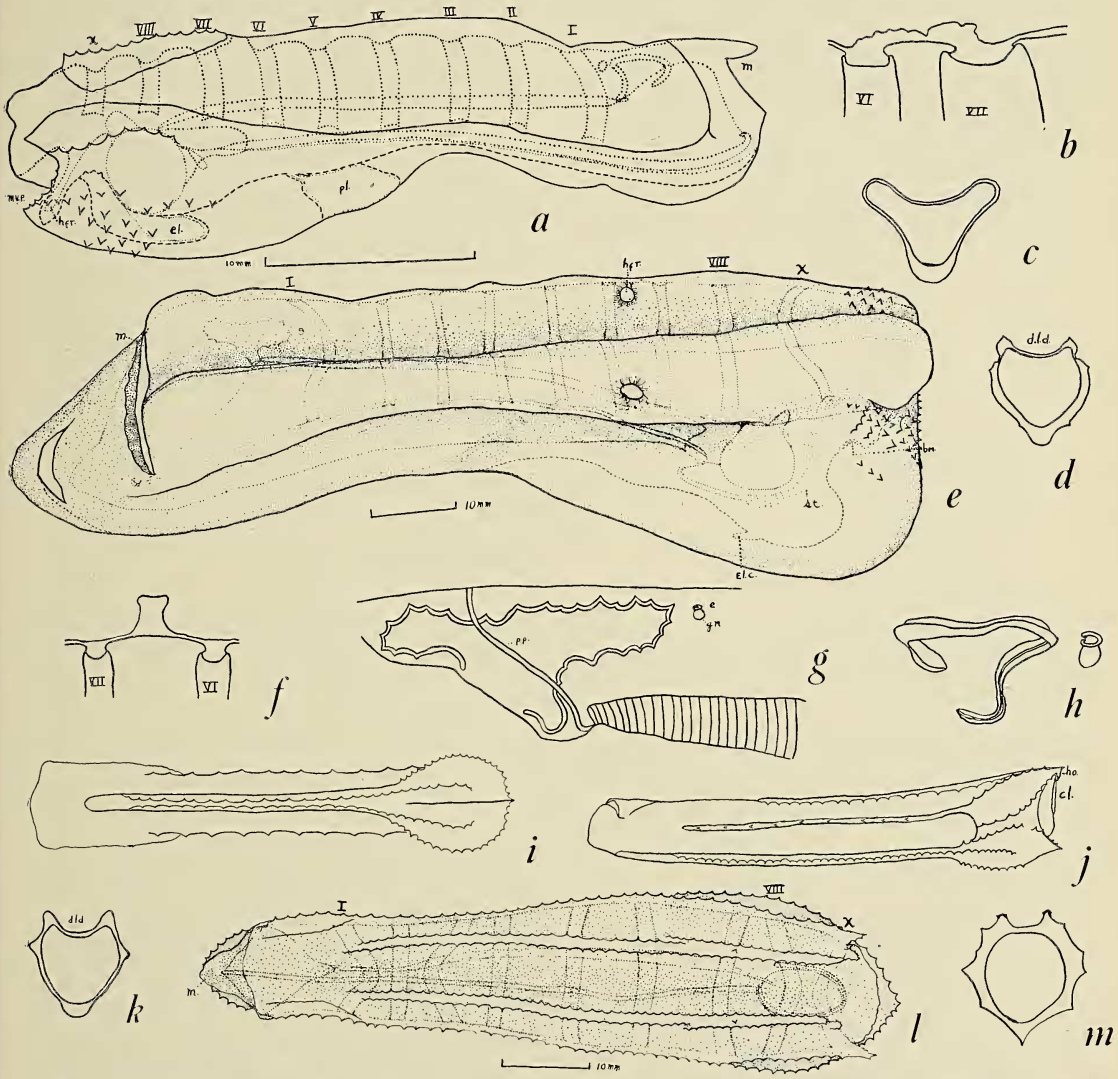


FIG. 13. *Salpa maxima*, solitary form. *a*, Smaller specimen, right side (the gut has been drawn up to reveal test cavities); *b*, dorsal attachment organ of a specimen similar to *a*, lateral aspect; *c*, same specimen as *a*, schematic cross section of test at level of M III; *d*, same specimen as *a*, schematic cross section of test at gut level; *e*, larger specimen, left side; *f*, same specimen as *e*, lateral aspect of dorsal attachment organ; *g*, same specimen as *e*, lateral aspect of ciliated groove and associated structures; *h*, same specimen as *a*, ciliated groove, ganglion and eye, dorsolateral aspect; *i*, echinate form, ventral aspect of test; *j*, same specimen as *i*, test from left; *k*, same specimen as *l*, schematic cross section of test at level of M III; *l*, another echinate specimen, dorsal aspect; *m*, same specimen as *l*, schematic cross section of test at gut level.

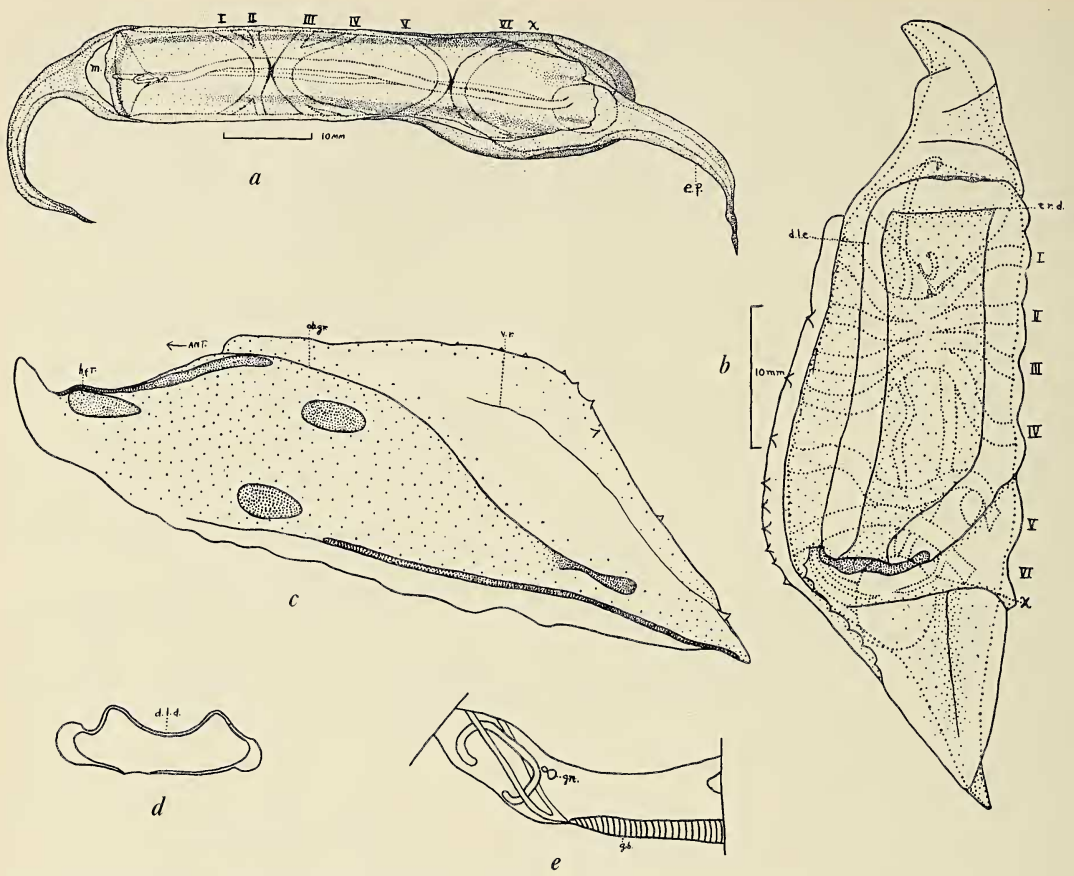


FIG. 14. *Salpa maxima*, aggregate form. *a*, Larger specimen, dorsal aspect; *b*, smaller (echinate) specimen, dorsal aspect; *c*, same specimen as *b*, ventral aspect of test; *d*, same specimen as *b*, schematic cross section of test at level of M IV; *e*, same specimen as *b*, left aspect of ciliated groove and associated structures.

anteriorly, turning posteriorly and usually rather closely encircling gut, then extending anteriorly again; a ventral posterior attachment organ usually present behind gut (Fig. 13*a*,*hft*).

AGGREGATE FORM: Over 10 specimens examined with length range of 10–112 mm. (Fig. 14). *Test:* In the typical (?) form, thick and smooth (Fig. 14*a*) in all areas; gut swelling prominent; end projections long or short; test bearing neither serrations, grooves, nor ridges; weak dorsal longitudinal depression and large ventral elevation present; gut cavity large, its margin smooth except for a V-shaped depression posteriorly. The most common form among POFI specimens is asymmetric, echinate, and smaller than the above-described form (Fig. 14*b*). Test thick in all areas; dorsal longitudinal depression limited by dorsal limiting elevations; transverse depression at base of upper lip; posteriorly a sparsely serrated dorsolateral ridge with a sparsely serrated lateral ridge ventral to it; a dorsal transverse groove posterior to cloacal aperture with a longitudinal groove extending from it posteriorly on the end projection; few spines on or near gut swelling; nonserrated ventral ridge on gut swelling; oblique groove in front of gut swelling; remaining anterior test thin, forming a shallow depression; attachment organs prominent, large; end projections broad, relatively short. *Muscles:* Six present, forming two groups, M I–IV and V–VI; IV and V may approach laterally and

even touch; muscles extending far toward ventral surface. Ventral lip sphincter 4 (M b_3) continuous. *Ciliated groove* (Fig. 14*e*): Anterior to M I, usually forming a large incomplete circle. *Viscera:* Gut compact, in condition C (Ihle and Ihle-Landenberg, 1933); embryo on right side dorsally between M V and VI.

The form *tuberculata* of Metcalf has not been found in the collections studied.

Individuals of the species of *Salpa* (solitary form) smaller than 2 centimeters have characteristic features. The two species can be distinguished by the presence in *S. maxima* of a large elaeoblast and cavity, a large ciliated groove with three bends, the usually separated muscles, and the absence of a ventral hook on the dorsal posterior test projection, whereas *S. fusiformis* has opposite characteristics (except for the presence of an elaeoblast in very young animals). When the animals are larger, these distinctions become gradually less apparent; the elaeoblast becomes reduced or resorbed, although in all specimens of *S. maxima* its test cavity remains; the ciliated groove of large *S. fusiformis* (47 mm. maximum length of POFI specimens) may have the same structure as that of *S. maxima;* the body muscles may either be grouped or distinct in both species; the internal "baumförmigen Fortsätzen" may be absent in *S. maxima;* large individuals of *S. maxima* may develop a ventral hook on the dorsal posterior test projection exactly as in *S. fusiformis* (Fig. 13*j*). Attachment organs, test, ganglion and eye, stolon, gut, and endostyle are either the same in both species or intergrade between them. The only structure that I have found never to intergrade is the cavity in which the elaeoblast lies in *S. maxima*. In all specimens examined, the elaeoblast cavity, although reduced in larger individuals, was present when the animal was considered, by other means, to be *S. maxima*. In all specimens considered to be *S. fusiformis*, even those as small as 11 millimeters, neither the elaeoblast nor its cavity was present. In small *S. fusiformis* the ciliated groove is a simple open one; in *S. maxima*, even in advanced embryos, the ciliated groove is large and possesses the characteristic three bends. Thus, the most important differences between the two species are (1) the presence in *S. maxima* of an elaeoblast cavity (both large and small individuals), and (2) the structure of the ciliated groove.

As a result of insufficient descriptions, it is impossible to determine from the literature whether the asperate forms described and fig-

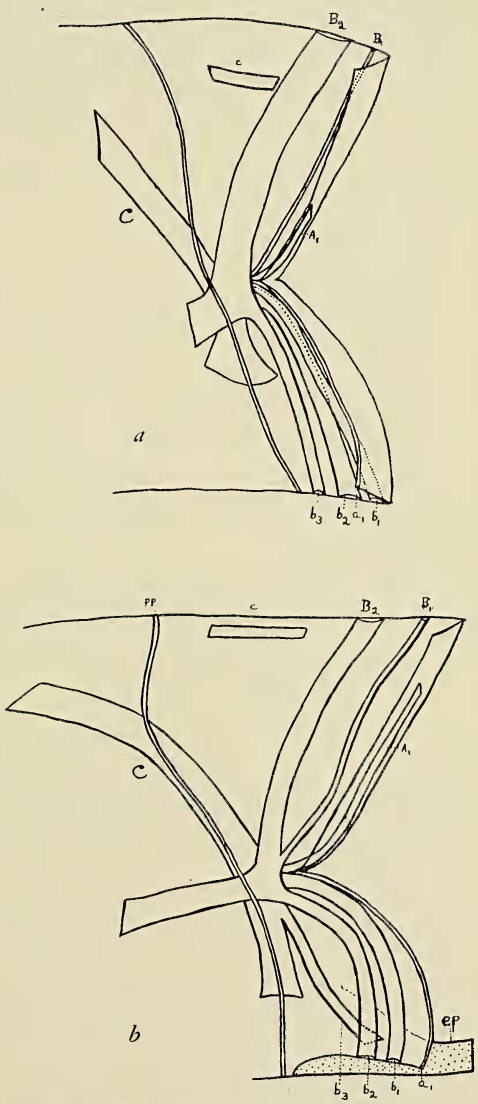


FIG. 15. Mouth musculature of left side, seen from inside. *a*, *Salpa maxima* agg.; *b*, *Salpa fusiformis* agg.

ured are *S. fusiformis* or *S. maxima* (see especially Herdman, 1888; Apstein, 1894*b;* Ritter, 1905; Ihle, 1910), although these were all considered *S. fusiformis*. I am inclined to regard the very large specimens described by some of these authors as *S. maxima*, but this is only speculation.

There is less difficulty in distinguishing the two species in the aggregate generation than in the solitary generation. Body muscle arrangement is a poor means of distinction (Stiasny, 1926). Nevertheless, it has been the main basis for differentiating *S. fusiformis* from other species. In the POFI collections, some individuals of *S. maxima* were found in which M IV and V touch laterally (usually considered a character of *S. fusiformis*), and many specimens of *S. fusiformis* were found in which, on either one or both sides, M IV and V do not touch. Other body structures, such as test, gut, position of embryo, and ciliated groove, are similar or intergrade between them. The differences in mouth musculature are the only certain means of distinguishing the two species in all specimens examined. In *S. maxima*, ventral lip sphincter 4 (M b_3) is continuous, whereas in *S. fusiformis* it is interrupted; there are also other differences as shown in Figure 15.

The great difference in size is usually a useful means of distinction between the species for both solitary and aggregate specimens.

Genus WEELIA gen. nov.

The genus is characterized as follows: In both generations, transverse ribs of the gill bar meet dorsally, becoming reduced in width sharply toward the ventral surface so that they are far separated from one another ventrally (Fig. 16); gut in state E of Ihle and Ihle-Landenberg (1933) in both generations; aggregate form with five body muscles that form two groups dorsally (M I–III, IV–V); body muscles interrupted ventrally in both forms; no independent muscle in the posterior projection of the aggregate form; solitary form with eight (rarely nine) body muscles of which M I–IV are either fused, joined by muscle strands, touch, or approach one another dorsally; body muscles may be split into branches laterally, sometimes are fused laterally, thus tending to vary considerably; no attachment organs in the solitary form (excluding lips and cloacal siphon); test of the solitary form (in POFI specimens) bears a varying number of thickened white patches that are arranged in rows; or, according to Brooks (1893), Sewell (1926), and Stiasny (1926), there are seven longitudinal ridges on the test—two dorsal, two lateral, and three ventral, with a posterior ridge joining the midventral ridge.

I regard *Salpa cylindrica* as sufficiently different from the other species of *Salpa* to be placed in a new genus, *Weelia*, named to honor Dr. P. B. van Weel of the University of Hawaii, who has contributed so significantly to the present study. The only known species, *Weelia cylindrica*, is the type.

Weelia cylindrica (Cuvier) 1804

Figs. 16*c*, 17*a–f*

Salpa cylindrica Cuvier, 1804: 381; Bomford,

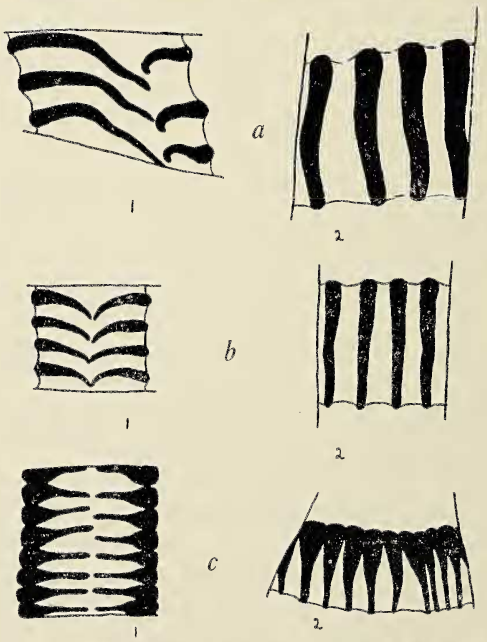


FIG. 16. Diagrams of a part of the gill bar of the solitary form. *a*, *Salpa maxima; b*, *Salpa fusiformis; c*, *Weelia cylindrica*. 1, ventral aspect; 2, lateral aspect.

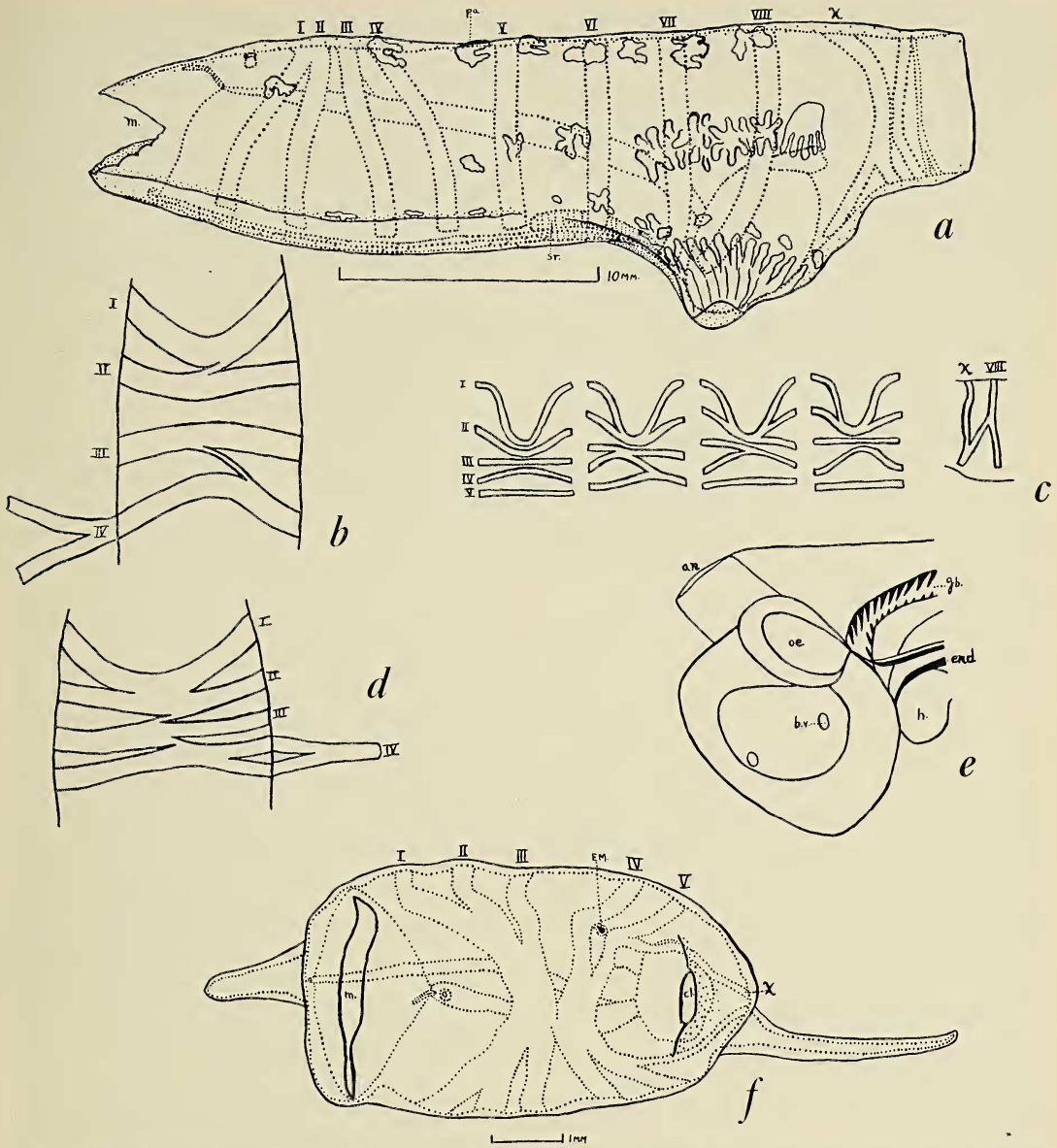


FIG. 17. *Weelia cylindrica*. *a*, Solitary form, left side; *b,c,d*, diagrams of muscle variation in the solitary form; in *b* and *d*, M IV is represented as being drawn out on one side (*c* after Sewell, 1926); *e*, gut of solitary form, right side; *f*, aggregate form, dorsal aspect.

1913: 243; Oka, 1915: 31; Ihle, 1935: 527–529; Tokioka, 1937: 223; Thompson, 1948: 161.

Iasis cylindrica Savigny, 1816: 235.

Salpa coerulescens Chamisso, 1819: 22.

Salpa elongata Blainville, 1827: 113.

Salpa garnotti [?] Lesson, 1830: 271.

Salpa truncata [?] Quoy and Gaimard, 1834: 588.

Salpa coerulea Quoy and Gaimard, 1834: 589.

Salpa (*Salpa*) *cylindrica* Metcalf, 1918: 93; Sewell, 1926: 77; Stiasny, 1926: 429.

SOLITARY FORM: Over 10 specimens examined with a length range of 14–38 mm. (Fig.

17*a*). *Test:* Glutinous, dorsally and laterally thin, ventrally thickened especially over the gut as gut swelling; from anterior point of gut swelling, two weak ridges lacking spines coursing shortly anteriorly and posteriorly on ventral surface of gut swelling; anteriorly a sparsely spined ridge encircling base of ventral lip; chin weakly developed; attachment organs absent; a varying number of white patches of thickened test most prominent posteriorly, especially over the gut, arranged in three rows on each side: (1) a dorsolateral row, (2) a lateral row, and (3) a ventrolateral row at edge of thickened ventral test continuing with patches over gut. *Muscles:* Eight (sometimes nine, as described by Sewell, 1926) body muscles, some of which may divide into two branches laterally; M I–IV approaching, fusing, or joining by means of fine strands of muscle dorsally, varying considerably (Fig. 17*b–d*); remainder of muscles usually equally separate from ane another except x, which may approach M VIII dorsally; all body muscles extend rather far ventrally; some may be fused, but usually are separate. *Ciliated groove:* Simple, elongate, straight or slightly bent. *Viscera:* Gut compact, in condition E of Ihle and Ihle-Landenberg (1933) (Fig. 17*e*); stolon club-shaped, straight (or undulating according to Thompson, 1948); transverse ribs of gill touching one another dorsolaterally; tapering sharply and becoming rather far separated ventrally. In species of *Salpa*, these ribs are separate along their entire length and taper gradually toward the ventral surface (Fig. 16).

AGGREGATE FORM: Over 10 specimens examined, with length range of 6–16 mm. (Fig. 17*f*). *Test:* Flabby, without permanent ridges or grooves; one anterior and one posterior asymmetric projection, which are usually short and stumpy, but may be elongate as in Fig. 17*f*. Eight attachment organs present according to Stiasny (1926), but only six were visible in POFI specimens. *Muscles:* Five body muscles; M I–III fused dorsally as are M IV and V; in all POFI specimens the two groups are joined dorsally (but may be distinct, according to other investigators); muscles extending rather far ventrally. *Ciliated groove:* Slightly arched, simple. *Viscera:* Gut compact, in condition E of Ihle and Ihle-Landenberg (1933); embryo on right side between M IV and V; gill as in solitary form.

This salp has been studied by many investigators, but only Brooks (1893) and, especially, Sewell (1926) have shown any of the great variation in muscle arrangement that occurs in the solitary form. The usual descriptions point out only that M I–IV approach or touch dorsally, the rest remain separate. The actual muscular arrangement may differ considerably from this condition (Fig. 17*b–d*). In regard to the test of the solitary form, Brooks (1893), Sewell (1926), and Stiasny (1926) described seven longitudinal ridges—two dorsal, two lateral, and three ventral—as well as a posterior ridge. In all specimens I have examined, however, there are only two longitudinal ventral ridges present, and they are much shorter than those described by the above-named investigators. Evidently, there is also a rather large amount of variation in test structure. Almost all specimens, both aggregate and solitary, in the POFI collections are separated from their tests. In only a few individuals did the tests remain on the animals. I was unable to find the ridges described by Stiasny (1926) on the test of the aggregate form.

Genus RITTERIELLA Metcalf, 1919

Solitary form with 10 to 24 body muscles, all of which are ventrally interrupted, except in *R. amboinensis* the first three or four form complete rings. Aggregate form with six body muscles that form groups dorsally. Transverse ridges of gill bar are separated from one another by a distance greater than 0.5 the width of the gill bar. Solitary form possesses a blood-forming organ.

Two species, *Ritteriella amboinensis* (type) and *R. picteti*.

R. picteti and *R. amboinensis* were first de-

scribed by Apstein (1904) from Amboina. In 1906, Ritter described what he regarded as a new species, *Cyclosalpa retracta* (= *R. retracta*). This, however, was regarded by Ihle (1910) as similar enough to *R. picteti* to be a doubtful species if an intermediate form were found. Komai (1932) described such an intermediate form, so that at present *R. retracta* is considered a synonym of *R. picteti*.

Ritteriella amboinensis (Apstein) 1904
Fig. 18*a–c*

Salpa amboinensis Apstein 1904: 651; 1906*b* (agg.): 166; Ihle, 1910: 34; 1912: 44.

Salpa (*Ritteria*) *amboinensis* Metcalf, 1918: 56; Sewell, 1926: 85.

Ritteriella amboinensis Ihle, 1935: 527–529; Tokioka, 1937: 222; Thompson, 1948: 126.

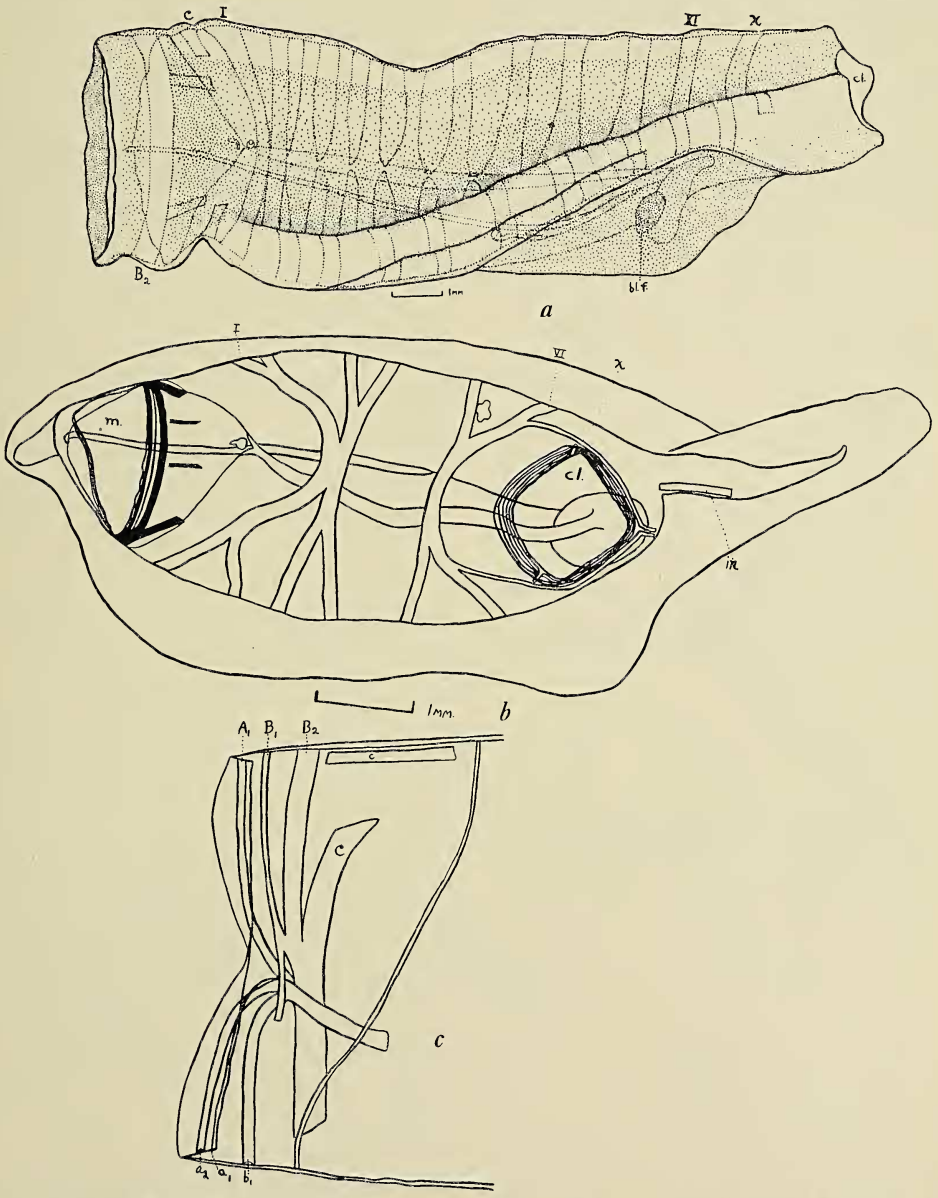


FIG. 18. *Ritteriella amboinensis*. *a*, Solitary form, dorsolateral aspect; *b*, aggregate form, dorsal aspect; *c*, aggregate form, mouth musculature of right side from inside.

[non] *Salpa amboinensis* Apstein, 1906*a:* 250; 1906*b* (sol.): 166.

SOLITARY FORM: Over 10 specimens examined with length range of 3 (embryos)–29 mm. (Fig. 18*a*). *Test:* Flabby, thin, especially over muscles; a rather thick, elongate gut swelling; there may be an additional swelling immediately over gut; no other permanent elevations or depressions. *Muscles:* Number of body muscles varies from 10 to 13, usually 11 or 12; number of muscles may be different on opposite sides of the body; M I–III touching dorsally as do X–XI and x; third upper lip sphincter muscle (B_2) distinct, large, continuous dorsally and ventrally; bow muscle interrupted dorsally, continuous ventrally; M I–III or IV forming rings; remainder of body muscles interrupted ventrally, becoming more widely interrupted posteriorly; all body muscles except I, II, X, and XI are joined dorsally by connecting bands of muscle; muscles relatively opaque and rather iridescent in all specimens examined. *Ciliated groove:* Simple, forming a crescent similar to that of *S. fusiformis* sol. *Viscera:* Gut rather compact, in condition A (Ihle and Ihle-Landenberg, 1933); stolon segmented only far anterior to gut, turning posteriorly at region of M V; a round or bean-shaped blood-forming organ present on left side of gut.

AGGREGATE FORM: Six specimens examined with a length range of 6–10 mm. (with projections) (Fig. 18*b,c*). *Test:* Flabby, glutinous; thin over whole body, slightly thicker over gut forming a rounded bulge; a general swelling of test material in gut area; end projections asymmetric, posterior one long, club-shaped, anterior one short, blunt. *Muscles:* Six body muscles of which M I–II and III–IV join dorsally into a group as do M V–VI; M I–II widely fused dorsally; all extend far toward the endostyle ventrally; a large, rather prominent independent muscle (*in*) on the posterior end projection under gut swelling, on right or left side according to position of animal on the stolon; this muscle much longer and more prominent than in any species of *Salpa;* M A_1 continuous dorsally; three ventral lip sphincters present. *Ciliated groove:* Situated vertically or almost so, a simple open structure. *Viscera:* Gut compact, in state D of Ihle and Ihle-Landenberg (1933); ribs or segments of gill bar relatively far separated; embryo attached beneath M V on right dorsal body wall.

Ritteriella picteti (Apstein) 1904
Fig. 19*a–f*

Salpa picteti Apstein, 1904: 655; 1906*a:* 252; 1906*b:* 168; Ihle, 1910: 43; 1912: 46.
Cyclosalpa retracta Ritter, 1906: 1.
Salpa amboinensis Apstein 1906*a:* 250; 1906*b:* 166.
[non] *Salpa amboinensis* Apstein, 1904: 651.
Salpa retracta Ihle, 1910: 40; 1912: 45.
Salpa (*Ritteria*) *retracta* Metcalf, 1918: 53.
Salpa (*Ritteria*) *picteti* Metcalf, 1918: 55; Sewell, 1926: 86.
Salpa (*Ritteriella*) *picteti* Komai, 1932: 65.
Ritteriella picteti Ihle, 1935: 527–529; Tokioka, 1937: 222; Thompson, 1948: 124; Berner, 1954.

SOLITARY FORM: Over 10 specimens examined with length range of 21–86 mm. (Fig. 19*a,b*). *Test:* Moderately thick over whole body with a slight elevation over the gut region; flabby and glutinous; no permanent elevations and depressions except over gut (Figure 19*a* represents an unusual condition in which there is present one lateral depression on each side; usually there is a single dorsal depression and no lateral ones). *Muscles:* Number varying from 13 to 24, including x and y, in the POFI specimens; number of muscles on one side usually different from number on opposite side; all body muscles continuous dorsally, interrupted ventrally; M I–V or VI usually connected by bands of muscle, remainder may be connected or distinct. *Ciliated groove:* Elongate, sinuous, but simple. *Viscera:* Gut in condition G (Ihle and Ihle-Landenberg, 1933), T-shaped with esophagus and

caecum forming right and left parts, respectively, of head of T, intestine forming posterior shaft of T; elongate, cylindrical, blood-forming organ located on left side, projecting from region of caecum dorsally, then bending anteriorly (abnormally posteriorly as in the figured specimen); stolon forming a slight bend and turning posteriorly at region of M VI–VIII.

AGGREGATE FORM: Two specimens examined, with length range of 18–23 mm., without end projections (Fig. 19*c–f*). *Test:* Flabby, glutinous, without permanent elevations and depressions except gut swelling which forms a large protrusion almost wholly independent of the rest of the body; end projections asymmetric, filiform. *Muscles:* Body muscles closely similar to those of *R. amboinensis* except wider and composed of more fibers (Berner, 1954); three sphincters in dorsal lip, of which the

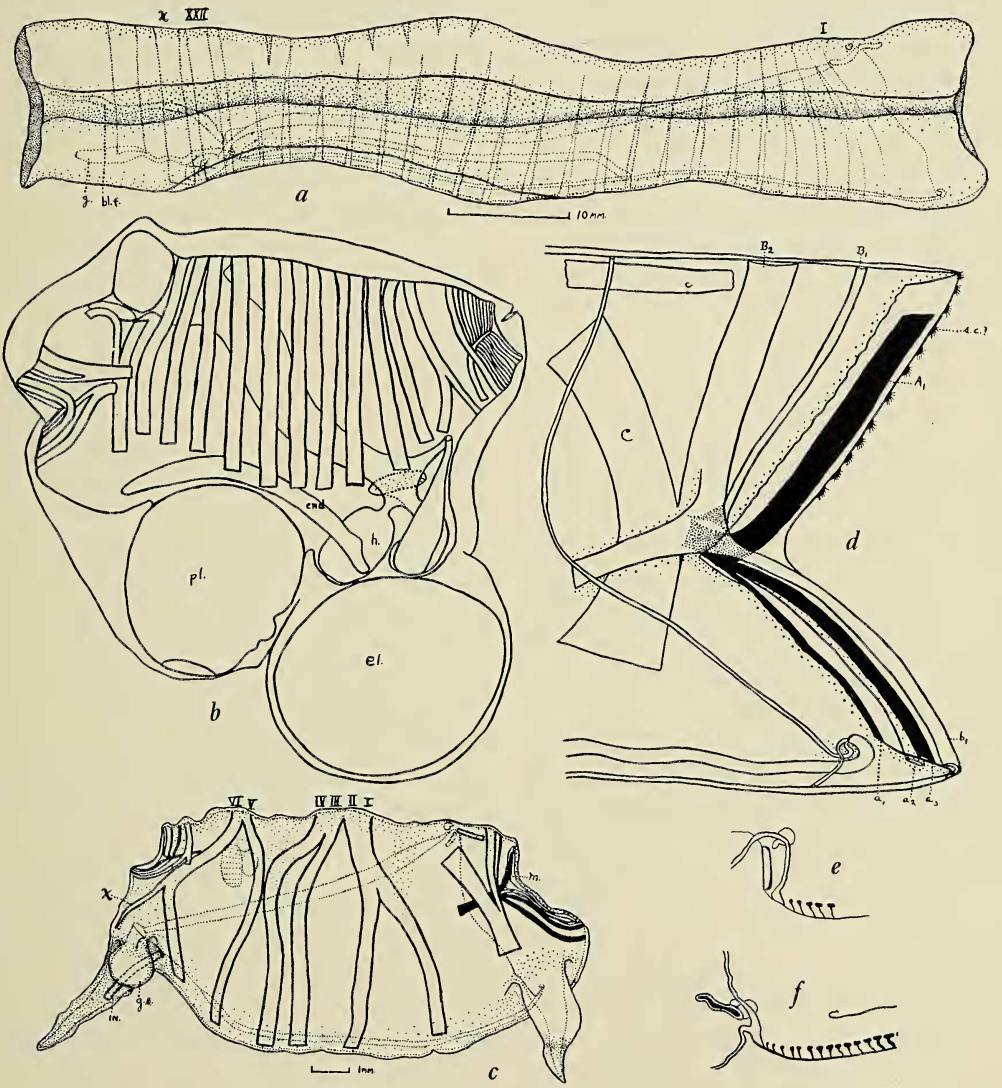


FIG. 19. *Ritteriella picteti. a*, Solitary form, right side; *b*, solitary form, left side of embryo (length, 1.3 mm.); *c*, aggregate form, right side; *d*, aggregate form, mouth musculature of left side from inside; *e*, aggregate form, ciliated groove, lateral aspect; *f*, aggregate form, ciliated groove, ventral aspect.

first is interrupted middorsally, the remainder continuous, and four continuous ventral lip sphincters; independent muscle large and conspicuous. *Ciliated groove:* Similar to that of *R. amboinensis* agg. *Viscera:* Similar to that of *R. amboinensis*, except that the endostyle extends almost to the gut in *R. picteti*, whereas it extends only to the level of M V or less in *R. amboinensis*.

The solitary forms of *R. picteti* and *R. amboinensis* are rather similar to one another. Descriptions of them, however, vary considerably and should be reviewed, as there is much overlapping between descriptions and probable errors in them. All descriptions agree in regard to gut structure (except for those of Apstein [1906*a*, 1906*b*] who evidently mistakenly identified his specimens as *S. amboinensis*). Ihle (1910) restudied these specimens and considered them to be *S. retracta*. They had the characteristic T-shaped gut structure of *R. picteti*.

In regard to muscle structure, however, there are a large number of contradictions. All past descriptions except Apstein's (1904) of *R. amboinensis* described M I–III as ring muscles. Apstein, however, in first describing the species, stated that the anterior muscles coursed almost to the endostyle and were thus interrupted. Ihle (1910) restudied these specimens that Apstein had described and stated for *R. amboinensis* sol. that "die 3 vorderen Körpermuskeln ebenso wie die Bogenmuskel ringförmig sind."

Sewell (1926), although not describing the condition, figured in *R. amboinensis* sol. M I–IV as ring muscles; in most POFI specimens here examined, M I–IV are ring muscles; in some specimens, only M I–III are rings.

Ritter (1906) emphasized the fact that in his specimen of *Cyclosalpa retracta* (=*R. picteti*), M 2–10 were completely continuous ventrally, thus ring muscles. This has not been observed in any other specimen of the species.

Apstein (1906*a*) described specimens, regarded by him as *S. amboinensis*, as possessing four "vollkommene Rundmuskeln," although in his earlier description (1904) of *S. amboinensis* all body muscles were considered to be ventrally interrupted. Ihle (1910) restudied these specimens that Apstein (1906*a*) had studied and identified them as *S. retracta*. He stated that with this species all body muscles were ventrally interrupted. Later, however, Ihle (1912) described the species *S. retracta* as follows: "Vordere Muskeln ringförmig. . . ."

In specimens of *R. picteti* described by Apstein (1904), Ihle (1910), Sewell (1926), Komai (1932), and Thompson (1948), all body muscles were described as ventrally interrupted. Apstein later (1906*a*, 1906*b*) made no mention of this condition even though he had done so in 1904. Ihle (1912), however, stated in regard to *R. picteti*, "Vordere Muskeln medio-ventral geschlossen." Also, Ihle (1935) characterized the genus *Ritteriella* as possessing 9–24 body muscles of which the "vorderen ringförmig sind."

Komai (1932) described a specimen of *R. picteti* in which all body muscles were ventrally interrupted. In regard to Ritter's (1906) description that *C. retracta* possessed nine ring muscles, Komai stated, "It is very doubtful whether one can put so much importance on that feature of the musculature in *R. retracta*, even if Ritter's observation on this point is warranted." I cannot agree with this statement, but rather believe that inconsistencies described have been the result of mistakes on the part of the observers. My conclusion is upheld by the POFI embryo, in which all body muscles and M C are ventrally interrupted.

The blood-forming organ of *R. amboinensis* has been described only as round or bean-shaped. In *R. picteti* (and *S. retracta*) it has usually been described as elongate, but Ihle (1910) described that of *S. picteti* as bean-shaped and that of *S. retracta* as variable in structure. Thus, this character perhaps is not important systematically.

Descriptions of the stolon also vary considerably. In *R. picteti* it varies from a spiral

(Apstein, 1906*a*, identified by him as *S. amboinensis*) to an elongate vermiform structure with a slight bend; in *R. amboinensis* it forms a wide sickle-shaped curve or is straight but may be slightly spiralled; thus, this organ also is perhaps not important systematically.

It is obvious from the literature that there has been a considerable amount of confusion in identifying the two solitary forms. Also obvious, both from the literature and POFI specimens, is the fact that these forms have a wide range of variability, perhaps more than any other salp, especially in muscle number and condition. I believe, however, that the differences in gut structure and in interruptions of the body muscles are important and valid differences. They are applicable to all POFI specimens, at any rate, except for the gut of the embryo of *R. picteti*.

The gregarious form of *R. amboinensis* has long been known (but that of *R. picteti* has only recently been described) by Berner (1954). Apstein (1904) first described the aggregate form of *R. amboinensis* rather inadequately, not describing the mouth or cloacal muscles. His figure does not permit accurate identification. Ihle (1910) studied this form next, describing both older chain forms and very young stolonic individuals. His descriptions are thorough and adequate for identification of *R. amboinensis* agg. He described and figured three sphincters in each lip (Taf. I, fig. 10) of the chain specimens. All these sphincters were described as uninterrupted. Metcalf (1918) based his description completely on that of Ihle (1910). He reproduced Ihle's figure 10 among others, thus showed *three* sphincters in each lip; but he described it as follows: "The oral muscles (Fig. 31) include a retractor and, in the upper and lower lips, two sphincters each. . . ." It may be thought that he considered the finer sphincters as only branches of one main sphincter, thus two in each lip, but in his other descriptions, each mouth muscle, no matter how small, was distinguished by a name and number. Therefore, he obviously misread Ihle (1910) and, although reproducing Ihle's figure correctly, he described the animal incorrectly. Thompson (1948) based most of his descriptions on those of Metcalf (1918) and repeated Metcalf's error in the description of *R. amboinensis* agg. Thompson's figure shows only two sphincters in each lip, but as the figure is of the whole animal, details were probably overlooked in the mouth musculature. He also reproduced Ihle's figures (1910) but described the animal inaccurately, although Ihle had clearly labeled the three sphincters in each lip.

Berner (1954) identified the aggregate form of *R. picteti* by the embryo held within them and distinguished the form chiefly by the following features: (1) the body muscles are composed of more fibers and are thus wierd, and (2) the lip muscles of *R. picteti* include three sphincters in each lip, whereas there are only two in *R. amboinensis*. He apparently carried on the error of Metcalf and Thompson in his statement that the aggregate form of *R. amboinensis* has two sphincters in each lip.

I have found two specimens of the aggregate form of *R. picteti* in the POFI collections as well as six specimens of *R. amboinensis* and thus have been able to make a thorough comparison.

The major differences noted are:

1. *R. picteti* possesses three dorsal lip sphincters (A_1, B_1, B_2) and four ventral lip sphincters (a_1, a_2, a_3, b_1), one of which, a_2, remains hidden beneath the more conspicuous a_3; in *R. amboinensis* there are three dorsal lip sphincters, one of which, B_1, is very small and thus inconspicuous, and the ventral lip also contains three.

2. As Berner (1954) showed, in *R. picteti* upper-lip sphincter 1 (A_1) is interrupted middorsally, whereas in *R. amboinensis* it is continuous.

3. The gut swelling of *R. picteti* is conspicuous and almost completely independent of the remainder of the body (as described in some specimens by Ihle, 1910; thus, if this

proves to be a useful difference, Ihle may have examined some specimens of *R. picteti* agg.), whereas in *R. amboinensis* it projects only slightly and is not independent of the remainder of the test.

4. The posterior end projection of *R. amboinensis* is large and club-shaped, whereas that of *R. picteti* is small and almost filiform.

5. The anterior end projection is short and blunt in *R. amboinensis*, whereas it is moderately long and filiform in *R. picteti*. Thus, if these last three differences are universal, these species deviate somewhat from the usual condition in salps in that the test is soft (but permanent structures are apparently present) and yet is useful in species distinction.

6. The endostyle extends further posteriorly in *R. picteti* than in *R. amboinensis*.

Both specimens of *R. picteti* contained embryos recognizable as this species, but the gut was not yet extended (Fig. 19*b*). No specimens of *R. amboinensis* contained embryos old enough to show structures nearing adult condition. The largest of these latter embryos (length, 0.3 mm.) contained nine recognizable body muscles, each of which, however, was widely interrupted dorsally and ventrally. A study of a nearly mature embryo from an aggregate *R. amboinensis* is thus desirable.

Genus METCALFINA Ihle and Ihle-Landenberg, 1933

Solitary form with 10–13 asymmetric, ventrally interrupted body muscles; these are all joined dorsally. Aggregate form with six ventrally interrupted body muscles, of which M V and VI are independent from other body muscles. Test of both forms is firm and bears serrated ridges.

One species, *Metcalfina hexagona*.

Metcalfina hexagona (Quoy and Gaimard) 1824

Figs. 20*a–d*, 21*a–d*

Salpa hexagona Quoy and Gaimard, 1824: 505; Bomford, 1913: 244; Oka, 1915: 30.
Salpa triangularis [?] Quoy and Gaimard, 1824: 511.
Salpa biensis [?] Blainville, 1827: 123.
Salpa lineata [?] Lesson, 1830: 268.
Salpa monotoma [?] Quoy and Gaimard, 1834: 591.

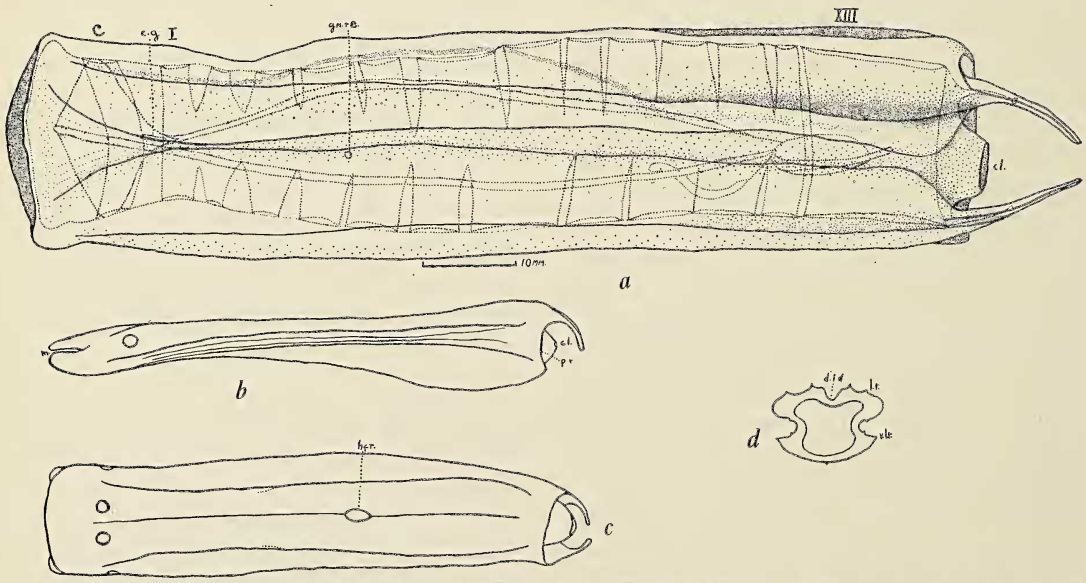


FIG. 20. *Metcalfina hexagona*, solitary form. *a*, Whole animal, dorsal aspect; *b*, test, left side; *c*, test, ventral surface; *d*, schematic cross section of test at level of ganglion.

Salpa (*Jasis*) *hexagona* Apstein, 1894*a:* 52.

Jasis hexagona Heider, 1895: 368.

Salpa (*Ritteria*) *hexagona* Metcalf, 1918: 62; Sewell, 1926: 87.

Metcalfina hexagona Ihle and Ihle-Landenberg, 1933: 199; Ihle, 1935: 527–529; Thompson, 1948: 129.

SOLITARY FORM: More than 10 specimens examined with length range of 48–117 mm. with end projections (Fig. 20). *Test:* Traustedt (1885) figured the test accurately; unfortunately, his figures were not copied completely by Apstein (1906*b*), Metcalf (1918), and Thompson (1948), who left out the test ridges so well shown by Traustedt. The description of the test here agrees with that of Traustedt, but he did not figure or describe the attachment organs described here. Test firm; one posterior projection on each side that contains a mantle process which bears a sucker on its tip. As Sewell (1926) pointed out, there are on each posterior projection five [minutely serrated] ridges. They are symmetrically located—one dorsal, two lateral, and two ventral. The lateral ridges of the projections are continuous with the posterior ridge of test encircling the cloacal siphon ventrally. There are 11 longitudinal ridges—four dorsal, six lateral, and one ventral (or four lateral and three ventral)—and one circular posterior ridge around the cloacal region ventrally, continuous with the posterior projections. In small specimens, all these ridges bear small or minute spines. In large specimens the spines are sparse and always minute. Chin and gut swelling moderately large. Attachment organs are relatively numerous on this solitary form; one disappears in the largest specimens. There are two anteroventral attachment organs at base of chin; a third, midventral and anterior to gut region, interrupts mid-

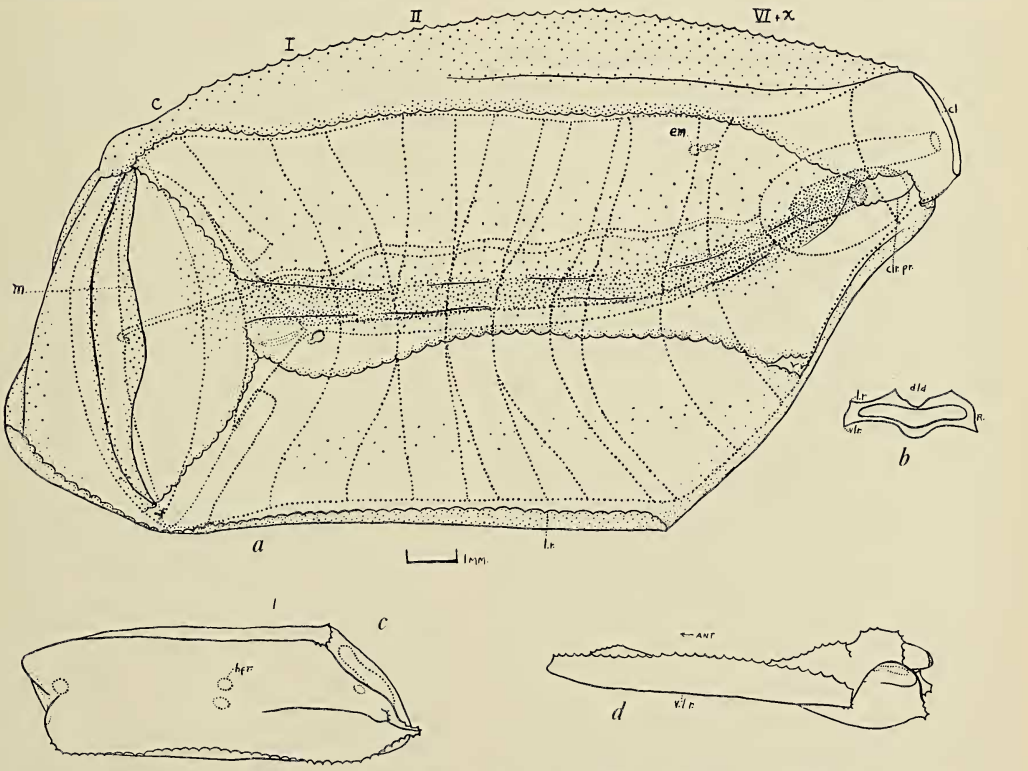


FIG. 21. *Metcalfina hexagona*, aggregate form. *a*, Whole animal, dorsal aspect; *b*, scheme of cross section of the test at M III level; *c*, test, ventral aspect; *d*, test, left side.

ventral ridge; it is absent in largest specimens; one lateral attachment organ on each side just behind angle of mouth. *Muscles:* Number varies, in POFI specimens ranging from 10 on one side and 11 on the opposite side to 12 and 13, respectively; muscles usually unequal in number on opposite sides; in POFI specimens, all body muscles irregularly continuous dorsally and connected dorsally by muscle strands except the last one, all interrupted rather widely ventrally (according to the figures of Traustedt, 1885, and Thompson, 1948, however, M I and II are distinct muscle bands); the last muscle much broader than other muscles; M C broad, continuous dorsally, widely interrupted ventrally. *Ciliated groove, ganglion and eye:* Ciliated groove elongate, straight, simple, located between M I and M C or under M C; ganglion and eye located far posteriorly, under M IV or V; eye a modified horseshoe (see Metcalf, 1918, fig. 39) with pigment at base and at each tip. *Viscera:* Gut moderately compact, in condition E (Ihle and Ihle-Landenberg, 1933); stolon forming a weak spiral, coursing anteriorly, bending and coursing posteriorly on left side of gut.

AGGREGATE FORM: More than 10 specimens examined with length range of 2 (stolon individual)–41 mm. (Fig. 21). *Test:* As with the solitary form, the aggregate form has been figured well by Traustedt (1885), Brooks (1893), and Apstein (1894*b*). Traustedt's figure, unfortunately, is of a dissected specimen, thus does not show the dorsal surface of the test. Test firm, asymmetric; middorsal depression thin, limited by weak grooves; dorsal limiting ridges on either side of depression, one always farther away from dorsal depression than other; these ridges continuing anteriorly into a circular ridge ringing the mouth widely; circular ridge on this side continuing posteriorly as lateral ridge ending after turning ventrally near level of gut; a prominent circular projection posteriorly over gut, flat on top and ridged; gut swelling and chin prominent; ventrolateral ridge not serrated except on posterior tip (no equivalent ridge on opposite side of body); on opposite side a ventrolateral ridge (equivalent to lateral ridge above), serrated; in ventral view, a prominent midventral ridge over gut swelling disappearing anteriorly, forming a small posterior projection; all ridges mentioned except ventrolateral ridge on one side (left side in figures) and midventral ridge rather strongly serrated; thus six longitudinal ridges, one anterior circular one, and one posterior one below the cloacal siphon; attachment organs usually six—one large one at each end, one smaller circular one just anterior and posterior, respectively, to the latter, and two smaller circular ones midventrally. *Muscles:* Six body muscles, all interrupted ventrally, continuous dorsally; M I–IV forming a group dorsally, M V and VI independent; M V wider than first four, M VI much wider than V; M C broad, anterior part continuous middorsally; posterior part branching off from latter, interrupted dorsally. *Ciliated groove:* Moderately elongate, simple. *Viscera:* Gut compact, in condition E (Ihle and Ihle-Landenberg, 1933); endostyle sinuous; two to five, usually four embryos present.

Genus THETYS Tilesius, 1802

Solitary form with 16–22, aggregate form with 5, weakly developed body muscles which are widely interrupted ventrally. Some of them are also laterally interrupted. Test firm, with many large spines over surface but without serrated ridges.

One species, *Thetys vagina*.

Thetys vagina Tilesius, 1802
Figs. 22*a–d*, 23*a–d*

Dagysa notata [part.] Gmelin, 1791: 3131.
Thetys vagina Tilesius, 1802: 150; Ihle, 1935: 527–529; Tokioka, 1937: 224; Thompson, 1948: 136.
Salpa tilesii Cuvier, 1804: 375.
Dagysa strumosa Home, 1814: 71.
Salpa costata Quoy and Gaimard, 1824: 504.

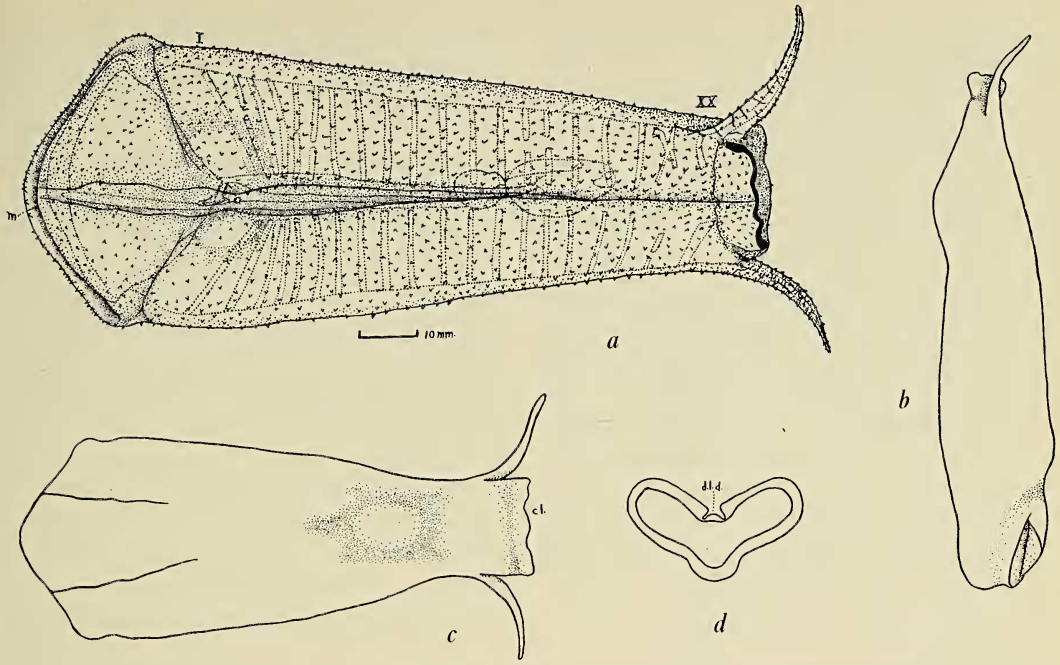


FIG. 22. *Thetys vagina*, solitary form. *a*, Whole animal, dorsal aspect; *b*, test, right side; *c*, test, ventral surface; *d*, schematic cross section of the test at gut level.

Salpa bigibbosa Quoy and Gaimard, 1824: 505.
Salpa gibbosa Quoy and Gaimard, 1824: 506.
Salpa infundibuliformis Quoy and Gaimard, 1824: 508.
Salpa costata-tilesii Traustedt, 1885: 379; Oka, 1915: 30.
Salpa sp. (?) n. sp. [?] Herdman, 1888: 62.
Jasis tilesii Lahille, 1890: 11.
Salpa (*Jasis*) *costata-tilesii* Apstein, 1894*a:* 50.
Salpa tilesii-costata Ritter, 1905: 70.
Salpa vagina Ihle, 1911: 587.
Salpa (*Thetys*) *vagina* Metcalf, 1918: 121; Sewell, 1926: 98; Stiasny, 1926: 446; Berrill, 1950: 299.

SOLITARY FORM: One specimen examined with length of 123 mm. without projections (Fig. 22). *Test:* Firm and thick except on inturned lips and on cloacal siphon; large spines occuring irregularly over whole surface; a prominent posterior projection on each side of cloacal siphon, containing tube of mantel epithelium with no sucker; dorsal depression limited by a groove on each side of a raised middle region, the whole limited by broad limiting elevations; shallow lateral depression; midventral elevation raised over gut and chin as swellings; transverse groove at base of dorsal lip, continuing laterally to angle of mouth; one swelling on each side of dorsal surface posterior to transverse groove; base of ventral lip with a weak circular depression; transverse groove at base of cloacal siphon; one short, weak, longitudinal depression crossing each side of chin ventrally. *Muscles:* Twenty weakly developed muscles (number varies from 16 to 22 according to Thompson, 1948); all interrupted dorsally and ventrally, often elsewhere, accompanied by prominent blood vessels; muscles not extending to ventral surface, but blood vessels do; M I–IV or VI converge dorsally. *Ciliated groove:* Forming a large open loop. *Viscera:* Gut large, compact, in state E (Ihle and Ihle-Landenberg, 1933); located far anteriorly, at about the posterior third of body; endostyle broad, straight; stolon coursing anteriorly, bending and coursing posteriorly on left side of gut (Traustedt, 1885).

AGGREGATE FORM: Seven specimens examined with length range of 33–71 mm. (Fig. 23). *Test:* Asymmetric, thick and firm except on lips and cloacal siphon; dorsal depression broad, extending from dorsal lip to above cloacal siphon; a broad dorsal limiting elevation on each side; transverse groove at base of dorsal lip; other transverse grooves and folds occuring incidentally over test; lateral depression shallow or forming deep grooves; ventral surface greatly thickened, especially over chin and gut swelling; large spines with a rather constant arrangement over test according to animal's location on the stolon; three longitudinal rows on dorsolateral elevation of one side, one row extending posteroventrally onto gut swelling; gut swelling with few spines on posteroventral region; on opposite side of test, two longitudinal rows on dorsolateral elevation continuing anteroventrally with a group of spines crossing lateral depression, extending onto chin; several spines present on posterodorsal and posteroventral regions of gut swelling; one group of spines extending transversely over dorsal lip; scattered spines in middorsal depression. Number of attachment organs varies, asymmetric in arrangement. *Muscles:* Five body muscles, interrupted dorsally and ventrally, extending only to sides of body; weakly developed, being interrupted in various places; M I–III converging dorsally but not touching; M V bifurcates; prominent blood vessels accompanying muscles. *Ciliated groove:* A large open loop. *Viscera:* Gut compact, in state E (Ihle and Ihle-Landenberg, 1933); endostyle narrow, sinuous; three or four embryos attached dorsally between M IV and V (Thompson, 1948).

Except for *Helicosalpa komaii* (230 mm.), the solitary form of this species is the largest of the salps (up to 226 mm. according to Traustedt, 1885). It was well figured (solitary form) by Traustedt (1885) and Stiasny (1926).

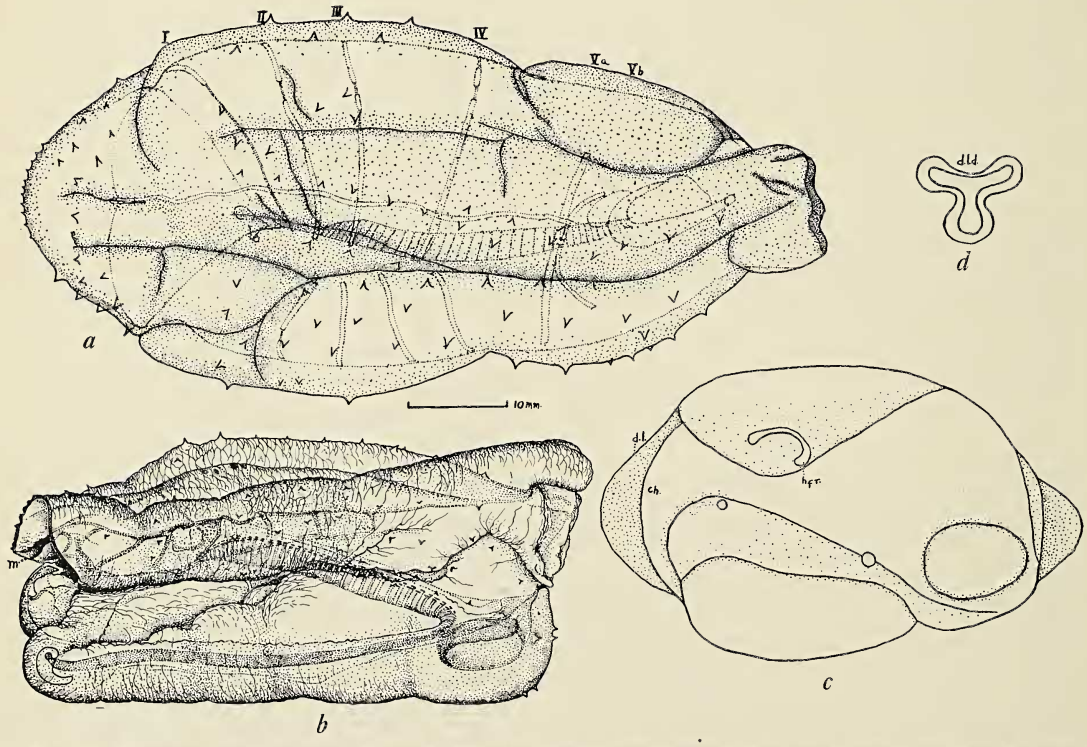


FIG. 23. *Thetys vagina*, aggregate form. *a*, Whole animal, dorsal aspect; *b*, another specimen, lateral aspect (length, 38 mm.); *c*, same specimen as *a*, ventral aspect of test; *d*, schematic cross section of test at level of M III.

The stolon individual (aggregate form) was well figured by Traustedt (1885) and Tokioka (1937). The preceding description (solitary form) agrees with their reports except for minor details.

Genus PEGEA Savigny, 1816

Four ventrally interrupted body muscles in both forms. Aggregate form with eight prominent, symmetrically arranged attachment organs.

One species, *Pegea confoederata.*

Pegea confoederata (Forskål) 1775
Figs. 24, 25

Salpa confoederata Forskål, 1775: 115; Bomford, 1913: 244.
Biphora confoederata Bruguière, 1789: 181.
Salpa gibba [?] Bosc, 1802: 178.
Salpa socia Bosc, 1802: 180.
Salpa scutigera Cuvier, 1804: 577.
Salpa octophora Cuvier, 1804: 577.
Salpa vivipara [?] Péron and Lesueur, 1807: pl. 31, fig. 3.
Pegea octofora Savigny, 1816: 235.
Salpa ferruginea Chamisso, 1819: 23.
Salpa informis Quoy and Gaimard, 1824 [*fide* Thompson, 1948].
Salpa bicaudata Quoy and Gaimard, 1827: 225.
Salpa laevis [?] Lesson, 1830: 273.
Salpa nephodea [?] Lesson, 1830: 275.
Salpa dolium [?] Quoy and Gaimard, 1834: 575.
Salpa femoralis [?] Quoy and Gaimard, 1834: 577.
Salpa scutigera-confoederata Traustedt, 1885: 362; Oka, 1915: 31.
Salpa quadrata Herdman, 1888: 84.
Pegea confoederata Lahille, 1890: 11; Ihle, 1935: 527–529; Tokioka, 1937: 230; Ihle and Ihle-Landenberg, 1938*a:* 107; Thompson, 1948: 143.
Salpa (*Pegea*) *scutigera-confoederata* Apstein, 1894*a:* 42.
Salpa (*Pegea*) *scutigera-confoederata* forma *bicaudata* Apstein, 1894*a:* 43.
Salpa confoederata-scutigera Ritter, 1905: 80.
Salpa (*Salpa*) *confoederata* Streiff, 1908: 32.
Salpa (*Pegea*) *confederata* Metcalf, 1918: 127; Berrill, 1950: 297.
Salpa (*Pegea*) *confederata bicaudata* Metcalf, 1918: 139.
Salpa (*Pegea*) *confoederata* Sewell, 1926: 100; Stiasny, 1926: 448.

SOLITARY FORM: More than 10 specimens examined with length range of 14–85 mm. (Fig. 24). *Test:* There are two different forms of this animal, the one characteristic of larger specimens, the other of smaller specimens. In the large form, test usually pear-shaped, smaller posteriorly, thick on ventral surface, especially over gut; dorsally a broad, slightly thickened elevation extending from upper lip to cloacal opening; this elevation limited laterally by one dorsolateral groove on each side; test very thin and flabby on lateral surface, therefore with no permanent shape; a prominent ventral elevation limited on each side by a ventrolateral groove; gut swelling prominent, produced as an additional swelling over the elaeoblast; test in all specimens examined not spiny, but earlier investigators have noted serrations on some specimens. In the small form, test pear-shaped, thick all over, firm, smaller posteriorly than anteriorly; on dorsal surface a shallow depression or deep groove extending from upper lip to cloacal opening; this depression limited by dorsal elevations; laterally a shallow depression extending from angle of mouth almost to region of gut; ventrally a rather strong elevation extending from lower lip almost to cloacal opening; this elevation further raised over elaeoblast as a disc-like bulge and bearing a far anterior small circular depression in which is located an attachment organ. The smaller form agrees more closely to the type set up by Stiasny (1926), but individuals are often different from his type. Thus, this animal deviates from the conclusion set up earlier here; that is, even though its test is firm and there may be grooves (but no ridges), these grooves probably are not permanent, and a definite "type"

cannot be established for it. Stiasny (1926) figured and described a longitudinal depression midventrally, limited to the anterior part of the test. I have not seen such a depression on any of my specimens, but in all the smaller ones there is a small circular depression for an attachment organ, which perhaps is what he saw. This is absent in larger specimens. The elaeoblast is relatively much larger in smaller specimens but is always a much-flattened disc. *Muscles:* Four body muscles; M I and II converging dorsally as do M III and IV; laterally all muscles diverging from one another, thus forming two X-shaped figures dorsally; muscles short. *Ciliated groove:* A large vertical loop whose ends approach one another anteriorly. *Viscera:* Gut compact, in state H (Ihle and Ihle-Landenberg, 1938*a*); elaeoblast forming a disc beneath gut; stolon encircling gut closely; endostyle weakly sinuous; on each side of endostyle at level of gut, a row of raised projections which have been noticed only by Ihle and Ihle-Landenberg (1938*a*), who described them as "Falten des Pharynxbodens" (*f* in Fig. 24). (These are not present in the aggregate generation.)

AGGREGATE FORM: More than 10 specimens examined with length range of 4–48 mm. (Fig. 25). *Test:* Loose, flabby, thin except around gut swelling and occasional thickened regions; gut swelling prominent, bearing ridges or elevations above and below a circular longitudinal depression which is very shallow; ventral surface usually with a rather thickened narrow elevation; thin membranous sheets of test material may extend loosely out from gut swelling; in bicaudate specimens, two triangular extensions of test containing mantle epithelium extending dorsolaterally over gut swelling, one to each side of cloacal opening; on all specimens, two lateral and two ventral attachment organs on each side of body, making a total of eight; attachment organs tubular, prominent, symmetrical. Stiasny (1926) figured prominent ridges both ventrally and dorsally in addition to the gut ridges. My specimens do not agree with this; as the test is flabby, presence of depressions and elevations is considered here to be a matter of chance. The cloacal siphon forms a weak flap. *Muscles:* As in the solitary form, M I and II form an X-shaped group dorsally, as do M III and IV; they extend only to the lateral surface. *Ciliated groove:* Forming a large loop whose ends approach anteriorly. *Viscera:* Gut compact, in state C of Ihle and Ihle-Landenberg (1933); endostyle sinuous; embryo on right dorsal region between M III and IV.

The subspecies *bicaudata* of Metcalf (1918) is perhaps only a slight modification of the typical form. Sewell (1926) stated: "I

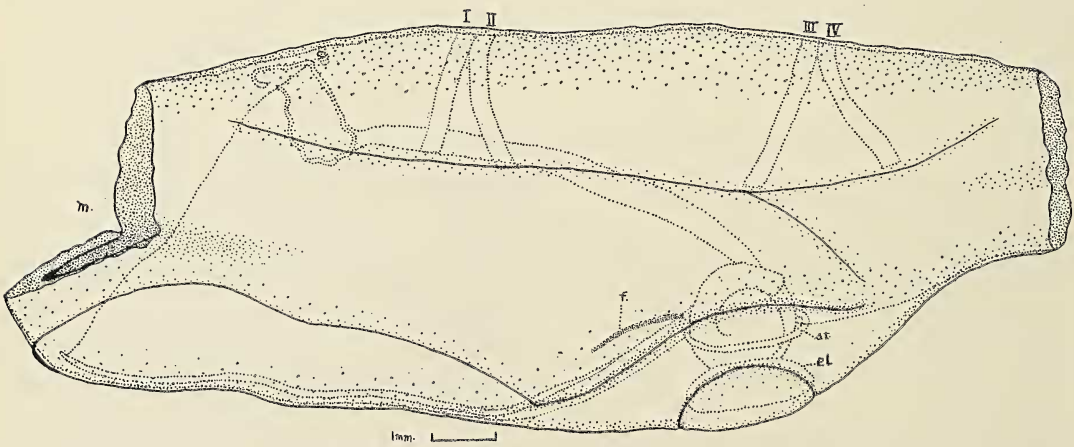


FIG. 24. *Pegea confoederata*, solitary form, left side.

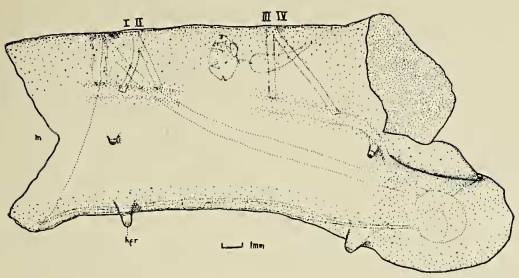


FIG. 25. *Pegea confoederata*, aggregate form, left side.

can see no justification for considering the *bicaudata* form to be even a variety, and much less a distinct subspecies, as Metcalf has done." Although I have seen only a few (all very small) specimens of this form, and thus little intergradation, Sewell's reckoning is considered probably correct here, and the bicaudate individuals are not given subspecific status.

Genus TRAUSTEDTIA Metcalf, 1918

Solitary form with 7 to 25 tentacles, aggregate form with two or three. Solitary form with five, gregarious form with four, body muscles that are widely interrupted ventrally.

One species, *Traustedtia multitentaculata*.

Traustedtia multitentaculata
(Quoy and Gaimard) 1834
Figs. 26*a–e*, 27*a–d*

Salpa multitentaculata Quoy and Gaimard, 1834: 596; Bomford, 1913: 244.
Salpa henseni Traustedt, 1893: 9.
Salpa verrucosa Apstein, 1894*b*: 12.
Salpa (*Traustedtia*) *multitentaculata* Metcalf, 1918: 147; Oka, 1921: 1; Sewell, 1926: 105.
Salpa (*Traustedtia*) *multitentaculata bicristata* Metcalf, 1918: 143.
Salpa (*Traustedtia*) *radiata* Metcalf, 1918: 152.
Salpa (*Traustedtia*) *henseni* Oka, 1921: 10–14.
Traustedtia multitentaculata Ihle, 1935: 527–529; Tokioka, 1937: 230; 1938: 234; Thompson, 1948: 147.

SOLITARY FORM: Five specimens examined with length range of 2–16 mm. (without projections) (Fig. 26*a*). *Test:* Thick, especially on crests, gut swelling, chin, and lips; in dorsal view, a raised median depression extending posteriorly to form the cloacal flap, anteriorly to the greatly thickened transverse ridges of the upper lip; continuing anterolaterally with a vertical elevation that joins its fellow of the opposite side midventrally under the chin; dorsal depression limited by grooves or depressions on each side which form the bases of the prominent dorsal limiting ridges (crests); crest covered with peculiarly shaped spines (see Fig. 26*c*, also Apstein, 1894, Taf. II, fig. 13), continuing with one break posteroventrally below and behind cloacal opening, meeting fellow of opposite side there; cloacal flap bearing a small projection on each side; each crest bearing a moderately long tentacle directed posteriorly; a posteroventral unpaired tentacle, which is doubtless the remains of the elaeoblast attachment as suggested by Thompson, projecting posteriorly; 10 other paired tentacles on posterior lateral to ventral anterior surface, some of which may be quite long; thus, a total of 25 tentacles present in this specimen; chin and gut swelling prominent; ventral lip bearing several ordinary spines and a median row of peculiar flattened spines (Fig. 26*d*); dorsal lip with two high transverse ridges at base; internal surface of dorsal lip bearing a series of longitudinal and transverse grooves and ridges that are serrated; chin smooth or serrated. *Muscles:* Three main muscle masses—first including fused M I–III, second large M IV, and third, M V and x; all except V branching on each side; M IV and V joining ventral cloacal muscles; all muscles extending only a short distance laterally. For descriptions of mouth and cloacal muscles, see Metcalf (1918), Oka (1921), Sewell (1926), and Thompson (1948). *Ciliated groove:* Simple, straight, located directly under ganglion and eye. *Viscera:* Gut forming an elongate loop, in state D of Ihle and Ihle-Landenberg (1933) (Fig. 26*e*); stolon forming a loose circle around gut; endostyle extending anteriorly to base of ventral lip.

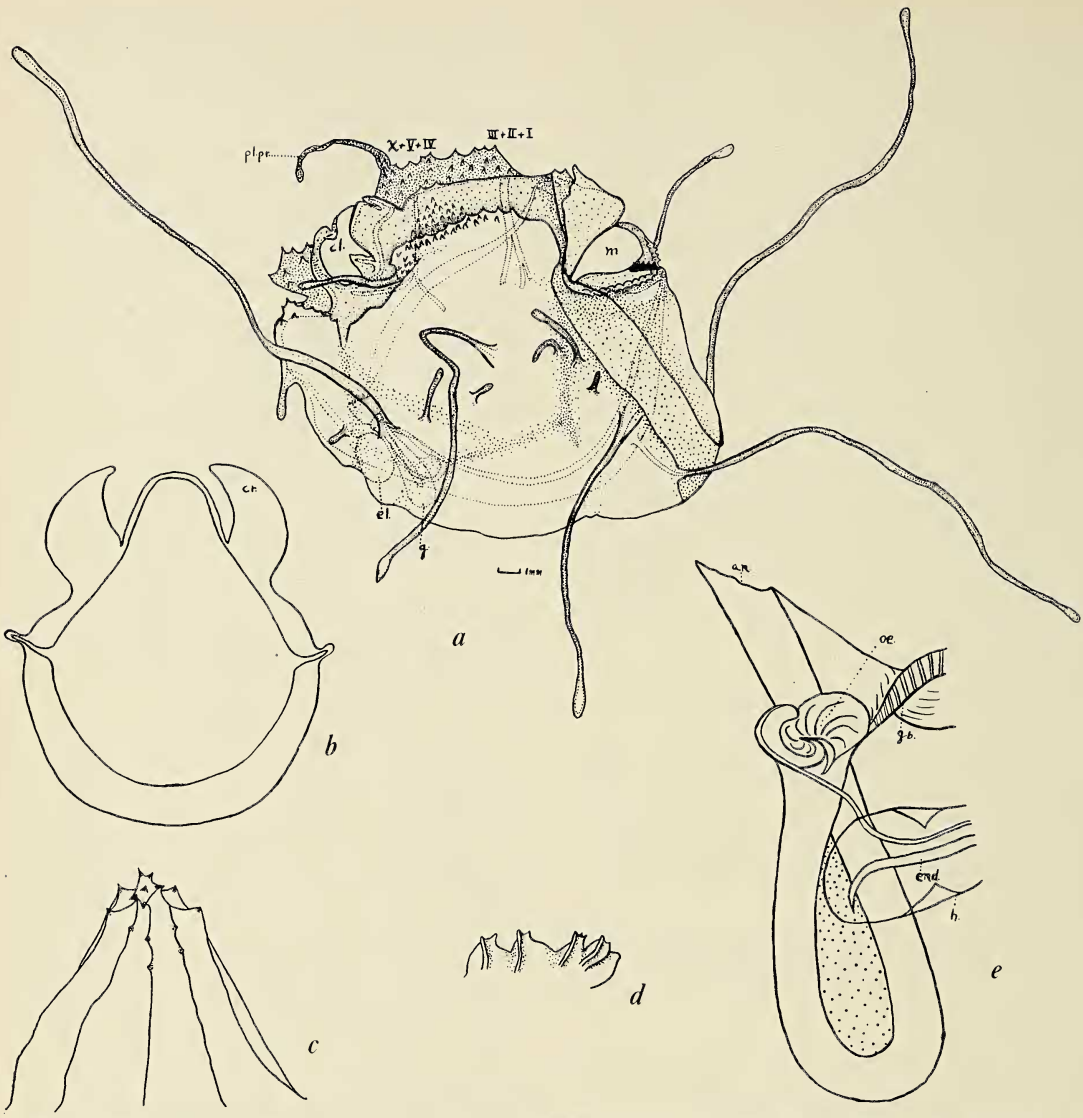


FIG. 26. *Traustedtia multitentaculata*, solitary form. *a*, Whole animal, right side, slightly from the front; *b*, schematic cross section of the test between M III and IV; *c*, body spine, 48×; *d*, ventral lip spines, 24×; *e*, gut from right side.

AGGREGATE FORM: Six specimens examined with length range of 4–13 mm. without projections (Fig. 27). The figures of Traustedt (1893), and especially Tokioka's descriptions and figures (1938), are excellent. The tentacles of this form are at most three, usually two. In addition, however, there are attachment organs that Sewell (1926) considered tentacles; this error was corrected by Thompson (1948). *Test:* Stiff, thick in all areas, especially on chin and gut swelling; mantle often far separated from test dorsally; weak dorsal elevation extending from base of cloacal flap to base of dorsal lip, limited by transverse grooves at these places; cloacal flap very large; laterodorsally, a bulging limiting elevation on each side of dorsal elevation, continuous to chin and posteriorly forming tentacle; tentacles three in young specimens: two lateral posterior, and one median posterior projecting

from end of gut projection; larger specimens without midposterior tentacle; Sewell (1926) and Tokioka (1938) figure those of the small individuals as possessing transverse constrictions, as do small POFI specimens, but the constrictions are much sparser here; tentacles flat at base, filamentous distally, with one dorsal ridge, and one ventral ridge which is continuous with posterior ridge that fuses with its fellow of the opposite side over gut; in lateral view, a broad lateral depression or narrow groove, ventral to dorsal limiting elevation, extending from base of tentacle to chin, which is smooth in POFI specimens, contrary to Sewell (1926, fig. 40) and the statement of Thompson (1948: 152); a broad ventral elevation extending from chin into gut swelling; posteriorly gut swelling forming a prominent projection bearing six large spines; four symmetrically arranged attachment organs on each side. The depressions and elevations of the test are variable. *Muscles:* Two main masses, of which the first consists of M I–II, the second of M III–IV and x; first muscle mass interrupted dorsally, second forming a distinct joint dorsally, as shown by Tokioka (1938); M IV does not help form ventral cloacal muscles, contrary to figures of Apstein (1904) and Thompson (1948); muscles extend only a short distance toward ventral surface. For a complete description of mouth and cloacal muscles, see Tokioka

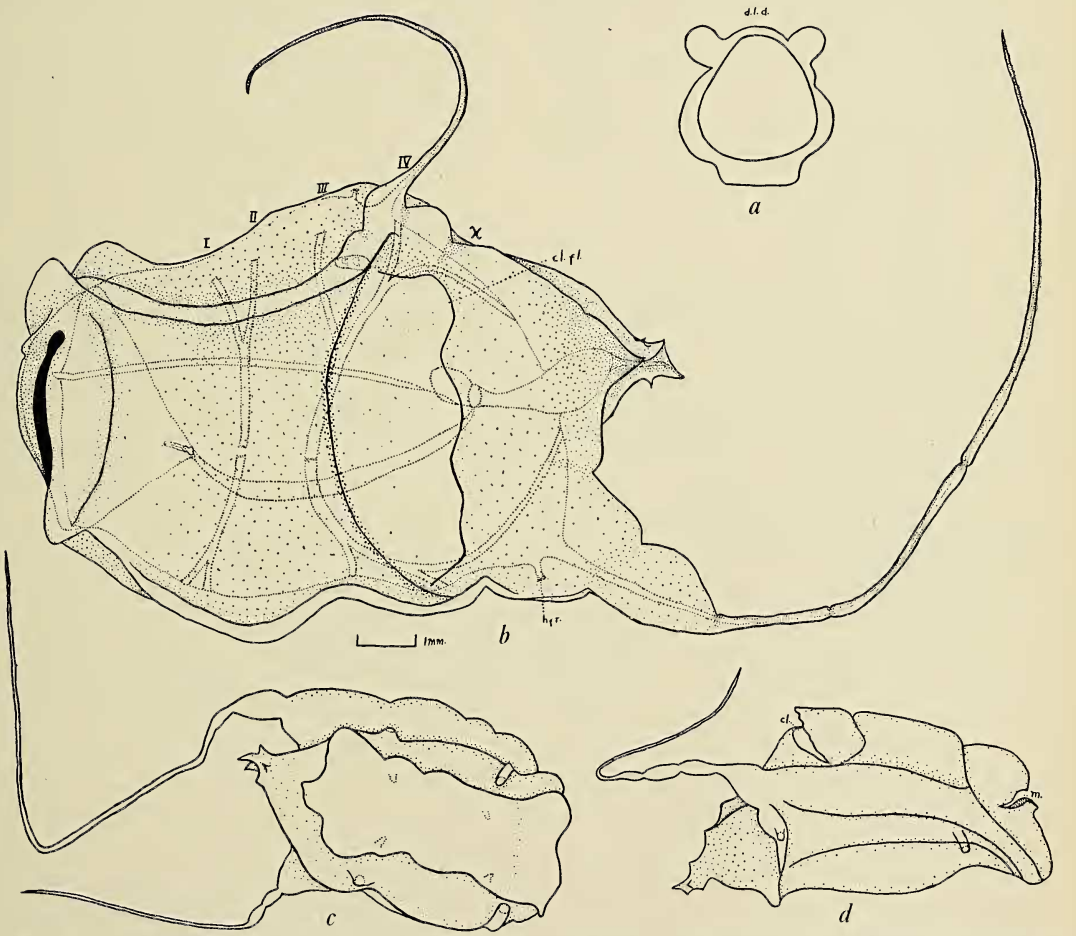


FIG. 27. *Traustedtia multitentaculata*, aggregate form. *a*, Schematic cross section of the test at level of M II; *b*, whole animal, dorsal aspect; *c*, test, ventral aspect; *d*, test, right side.

(1938). *Ciliated groove:* An open crescent; a broad languet below ciliated groove at junction with gill (Tokioka, 1938, fig. 5). *Viscera:* Gut forming elongate loop in which course of intestine is obscured by large number of testis lobules; in condition D of Ihle and Ihle-Landenberg (Tokioka, 1938); gut connected by long mantle projection with posterior gut projection; the mantle projection extending into median posterior tentacle, if present, as shown by Tokioka (1938); endostyle weakly sinuous; embryos two, lateral to joint of M III–IV on right side.

All the solitary forms described by Metcalf (1918) are probably one species, as Sewell (1926) believed. Oka (1921), however, recognized two species, *Salpa* (*Traustedtia*) *multitentaculata* and *S.* (*T.*) *henseni*, the latter being Metcalf's *S.* (*T.*) *radiata*, on the basis of the presence of eight tentacles in the former (according to my classification, 13, as he did not include in his count two paired and one unpaired pointed processes which are essentially similar to tentacles) and 20–23 in the latter. The conclusion that there is only one species is supported by the great variation in number of tentacles (varying from 7 to 25 in POFI specimens) and the probability that the radiate forms described by Apstein (1906*a*) and Dober (1912) simply were flattened dorsoventrally, giving the impression of a radiate form; this probably also explains the horizontal position of the gut of these specimens, as Sewell (1926) remarked. Sewell stated that differences in details of musculature are often due to conditions of preservation, which perhaps is the cause of differences described by Metcalf (1918). Both Oka (1921) and Sewell (1926) considered Metcalf's subspecies *bicristata* to be invalid. In POFI specimens the crested condition is one of intergradation, but crests are always present, apparently due to age differences. In one small (2 mm.) individual the crests are very small; they become more pronounced in larger individuals.

The only basis for considering the various forms distinct, according to Oka (1921) and Sewell (1926), is the different number of tentacles. Sewell (1926) distinguished between "true tentacles" and projections that penetrate the test but do not extend beyond the body margin. This, however, is probably only a condition of age and is not considered a useful distinction except for descriptive purposes. Oka (1921) remarked on the probable similarity of his "tentakeln" and "kurze . . . Anhänge" which projected from each sidewall of the cloacal opening. He also referred to "verborgene Tentakel" (those projecting into the crests and the unpaired posterior one). He did not describe any other projections. In the largest POFI specimen (Fig. 25*a*) all projections are of the true tentacle type, although many project only slightly beyond the test margin. In Sewell's (1926) and Thompson's (1948) specimens, there were nine tentacles present, including those not projecting beyond the body margin; in Apstein's (1894*b*) specimen there were eight, but, as Sewell (1926) remarked, there possibly were 13; in Metcalf's (1918) specimen and in Oka's (1921), 13 tentacles; and in Apstein's (1906*a*) and Dober's (1912) specimens, there were 20 and 23 tentacles present. Sewell (1926) thought there was a possibility that the differences were due to either geographic variation or variation in size. POFI specimens seem to confirm the latter conclusion as the number of tentacles is less with the smaller individuals and greater with larger ones. The smallest (2 mm.) specimen examined bore *no* "true tentacles" but bore seven mantle projections: one unpaired posterior; one pair of posterolateral projections (the "posterior tentacles" of Sewell and Oka and tentacle 6 of Metcalf); one pair of projections in the cloacal siphon (5 of Metcalf); one pair in the posterior part of the crests (4 of Metcalf).

Further, in a specimen of 7 millimeters length, the projections are still not "true tentacles." This specimen is so poorly preserved, however, that I am unable to ascertain the number of projections present.

In another specimen, 11 millimeters long,

the same relationships exist as in the 2-millimeter specimen described above, except the posterolateral projections (6 of Metcalf) are true tentacles and of the same length as the body.

In the largest specimen examined (16 mm.) there are 25 tentacles, as described above.

Thus, it is my belief that the tentacles also do not show variations that would lead to the separation of any of Metcalf's forms from the main species. It would be desirable to re-examine some of the larger specimens (for example, Oka's specimen of 23 mm. length), described as possessing 13 or fewer tentacles, with the use of toluidin blue. If these large specimens actually possess only 13 or less tentacles, then *T. henseni* should probably be recognized also, as Oka (1921) has done.

All aggregate forms described to the present time have been regarded as only one species, *T. multitentaculata*, and all POFI specimens agree with this conclusion.

Genus THALIA Blumenbach, 1810

Solitary form with five body muscles of which the first four form rings; aggregate form with five ventrally interrupted body muscles, with a short endostyle. Languet present in both forms ventral to the ciliated groove.

Two species, *Thalia democratica* (type) and *T. longicauda*. The latter species has not been found in the collections studied.

Thalia democratica (Forskål) 1775

Figs. 28*a–e*, 29*a–f*

Salpa democratica Forskål, 1775: 113; Bomford, 1913: 244.
Salpa mucronata Forskål, 1775: 114.
Biphora democratica Bruguière, 1789: 180.
Biphora mucronata Bruguière, 1789: 181.
Salpa cyanogaster [?] Péron and Lesueur, 1807: fig. 3.
Thalia lingulata Blumenbach, 1810: (30).
Salpa spinosa Otto, 1823: 303.

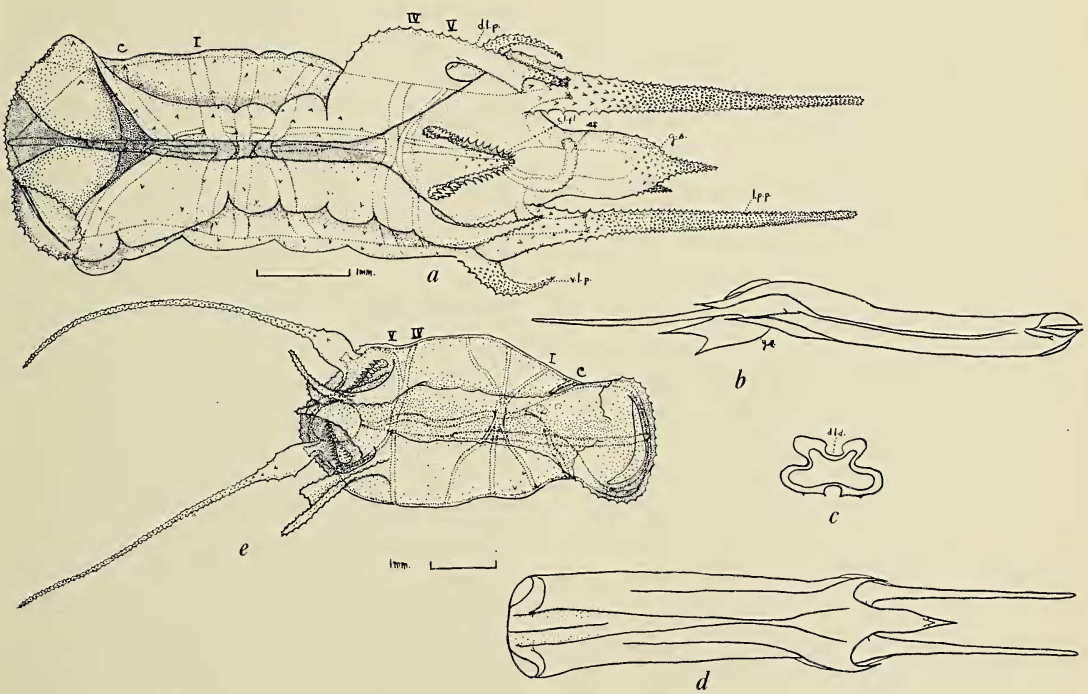


FIG. 28. *Thalia democratica*, solitary form. *a*, Echinate form, dorsal aspect; *b*, another specimen, test, right side; *c*, same specimen as *b*, schematic cross section of test at level of M III; *d*, same specimen, test, ventral surface; *e*, nonspiny form, dorsal aspect.

Salpa rhomboides [?] Quoy and Gaimard, 1824: 510.
Salpa rhomboidea [?] Blainville, 1827: 115.
Dubreuillia cirrhosa Lesson, 1830: 278.
Salpa pyramidalis [?] Quoy and Gaimard, 1834: 593.
Salpa caboti Desor, 1848: 75.
Salpa democratica-mucronata Traustedt, 1885: 365.
Thalia mucronata Lahille, 1890: 11.
Salpa (*Thalia*) *democratica-mucronata* Apstein, 1894*a:* 44.
Thalia democratica Heider, 1895: 368; Ihle, 1935: 527–529; Thompson, 1948: 139.
Salpa (*Salpa*) *mucronata* Streiff, 1908: 38.
Salpa (*Thalia*) *democratica* Metcalf, 1918: 109; Sewell, 1926: 92; Stiasny, 1926: 441; Berrill, 1950: 291.
Thalia democratica var. *orientalis* Tokioka, 1937: 226.
Thalia democratica var. *orientalis* forma *echinata* Tokioka, 1937: 229.

SOLITARY FORM: More than 10 specimens examined with length range of 4–9 mm., without projections (Fig. 28). *Test:* The echinate form (Fig. 28*a*) is discussed first. Test thick, especially over gut; gut swelling bearing two projections, one posterior and one ventroposterior; one usually long, lateral posterior projection on each side of body having no ridges but bearing many minute spines; one dorsolateral projection on either side of cloacal flap (atrial palp of Tokioka, 1937), ridged, bearing minute spines; each dorsolateral projection bearing a truncate medial portion extending posteriorly; one ventrolateral projection, usually smaller than the dorsolateral projection, extending posteriorly on each side of gut region; each a simple projection bearing minute spines; latter may be lacking, as Tokioka (1937) reported; thus, a total of six posterior projections of body and two of gut swelling; anteriorly, test truncate, ringed by an echinate ridge, with anteriorly projecting lip flaps; transverse dorsal groove at base of dorsal lip lying posterior to two bulges, one on each side of dorsal depression; dorsal depression widening anteriorly and posteriorly, limited by dorsolateral limiting elevations that continue posteriorly into lateral ridges of dorsolateral projections; in posterior widening of dorsal depression, high triangular cloacal flap projecting posteriorly, bearing a dorsal echinated ridge on its margin, a ventral heavily fringed margin below; ventral lip of cloacal opening similarly fringed, margined by a deep transverse groove; a deep lateral depression (seldom, a groove) present; a ventrolateral elevation, continuous with ventrolateral projections, coursing anteriorly; ventral surface bearing a midventral depression limited by midventral limiting ridges originating at ventrolateral projections; a prominent short midventral ridge present beneath chin. The smooth form is much like the above, having the same projections on the posterior end (often the ventrolateral projections are absent as in Fig. 28*e*), same cloacal flap structure, and the anterior ridge around the mouth; dorsal depression and limiting ridges present (these may be only elevations). The test, however, is not spiniferous ventrally and is sparsely so dorsally; it is thin and flabby. The muscles of this form are narrower than those of the echinate form. *Muscles:* One large bow muscle (C) interrupted dorsally, continuous ventrally; five body muscles present; M I–IV continuous dorsally and ventrally; M V continuous dorsally, narrowly interrupted ventrally (Metcalf, 1918, says M V is continuous ventrally, but all other investigators described it as interrupted, as here); M I–III converge in midline dorsally as do M IV and V, thus forming two dorsal groups; M III and IV converge, usually touch midventrally. *Ciliated groove:* Far separated from ganglion and eye, bearing a languet projecting ventrally into the pharyngeal cavity. *Viscera:* Gut elongate and U-shaped, in state B (Ihle and Ihle-Landenberg, 1933); projecting far into gut swelling; endostyle extending only from level of M III forward; stolon forming a close circle or spiral around gut.

AGGREGATE FORM: More than 10 specimens examined with length range of 1–12 mm. (Fig. 29). *Test:* The echinate form (Fig. 29*a*) is discussed first. Test asymmetric, thick, stiff, with prominent, sparsely spiniferous ridges and with deep grooves and depressions; middorsal depression (limited to anterior region in some specimens) limited by spiniferous dorsal limiting ridges; depression constricted at base of dorsal lip, widening anteriorly around mouth; a transverse ridge in front of cloacal flap; cloacal flap hemispherical rather than triangular, fringed as in solitary form; gut swelling projecting in a point toward rear (this may be very long in young specimens as figured by Apstein, 1906*a*, Sewell, 1926, and Tokioka, 1937), bearing five spiniferous ridges that are usually symmetrically arranged; lateral ridges asymmetric, spiniferous; anterior end almost truncate; ventrally a single deep groove in a broad depression cut off anterolaterally by an oblique spiniferous ridge that connects with anterior end; gut swelling with a strong ventral ridge; attachment organs varying in number, elongate and filiform (but usually not projecting beyond test margin). There is a great amount of test variation as reported by Stiasny (1926). In the smooth form (Fig. 29*e*), test flabby, without spines of any kind, with long attachment organs usually projecting beyond test outline; no permanent ridges or grooves, but there may be depressions and elevations; protruding gut swelling; cloacal flap with fringes. *Muscles:* Five body muscles; M V relatively narrow; all muscles continuous dorsally, interrupted ventrally; M I–III in contact dorsally, forming a group as do IV and V. *Ciliated groove:* Far anterior; simple, with a languet projecting into pharynx. *Viscera:* Gut compact, in condition B (Ihle and Ihle-Landenberg, 1933); elongate; protruding far into gut swelling; endostyle short, extending anterior to level of M I or II only; embryo far behind M IV on right ventral body wall.

The variety *orientalis* recognized by Tokioka (1937) is based on the following differences:

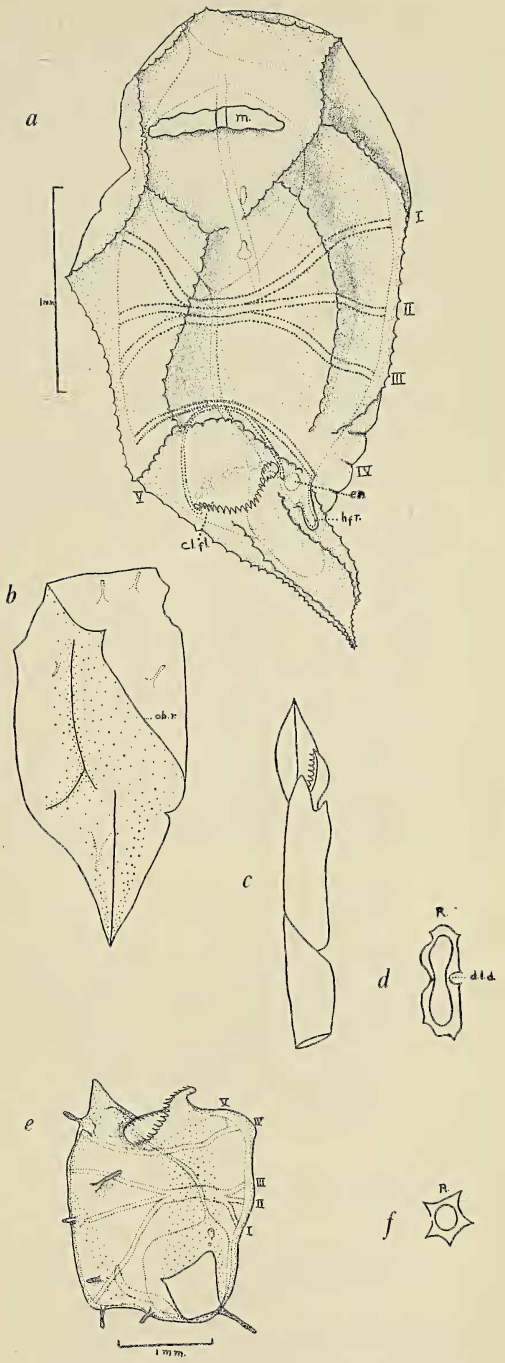


FIG. 29. *Thalia democratica*, aggregate form. *a*, Echinate form, dorsal surface; *b*, same specimen, test, ventral surface; *c*, same specimen, test, right side; *d*, same specimen, schematic cross section of test at level of M III; *e*, smooth form, right side, slightly dorsal; *f*, scheme of cross section of test at gut swelling of specimen in *a*.

small size; atrial palp bifurcated; smooth appearance of the testis lobes. Moreover, he distinguished the form *echinata* on the basis of "the existence of several spiniferous ridges on the testa." Sewell (1926) also distinguished a spiniferous form and found them to be uniformly of a smaller size than Atlantic specimens. In the POFI collections there are also two forms distinguishable on the basis of test differences, the one an echinate form, the other a smooth form; both are small. There are, however, among solitary individuals, intergrading degrees of echination, but conclusions on the validity of Tokioka's variety and form deserve further study, especially of a series of specimens from different oceans.

Although this species is the most common salp of warm seas (Apstein, 1906*a*), it is not one of the better known in regard to test structure. Apstein (1906*a*) figured the echinate aggregate form well, as did Stiasny (1919) and Tokioka (1937). The smooth form of both generations was well figured by Stiasny (1926). It is felt, however, that the figures in the present report are more thorough than previous ones as a result of staining.

Genus Iasis Savigny, 1816

Solitary form with five broad, dorsally and ventrally interrupted body muscles and with a broad M C. Aggregate form with five body muscles of which the first is interrupted dorsally and ventrally, the remainder only ventrally; M V is branched into two parts on the right side.

One species, *Iasis zonaria*.

Iasis zonaria (Pallas) 1774
Fig. 30*a–i*

Holothurium zonarium Pallas, 1774: 26.
Salpa polycratica Forskål, 1775: 116.
Biphora zonaria Bruguière, 1789: 182.
Salpa zonaria Chamisso, 1819: 12; Bomford, 1913: 245.
Salpa cordiformis Quoy and Gaimard, 1827: 226.
Salpa microstoma Quoy and Gaimard, 1827: 226.
Salpa unicuspidata Blainville, 1827: 116.
Salpa quadrangularis [?] Lesson, 1830: 268.
Salpa tricuspidata [?] Lesson, 1830: 272.
Salpa cordiformis-quadratica Vogt, 1854: 7.
Salpa cordiformis-zonaria Traustedt, 1885: 382; Oka, 1915: 30.
Salpa nitida [?] Herdman, 1888: 81.
Jasis polycratica Lahille, 1890: 11.
Salpa (*Jasis*) *cordiformis-zonaria* Apstein, 1894*a:* 51.
Jasis zonaria Heider, 1895: 368.
Salpa zonaria-cordiformis Ritter, 1905: 76.
Salpa (*Salpa*) *zonaria* Streiff, 1908: 45.
Salpa (*Iasis*) *zonaria* Metcalf, 1918: 100; Stiasny, 1926: 434; Berrill, 1950: 295.
Salpa (*Jasis*) *zonaria* Sewell, 1926: 88.
Iasis zonaria Ihle, 1935: 527–529; Tokioka, 1937: 223; Thompson, 1948: 132.

SOLITARY FORM: More than 10 specimens examined with length range of 16–51 mm. (Fig. 30*a–e*). *Test:* Firm, elongate; moderately thick; mouth a broad slit; dorsal depression extending to base of upper lip, limited by dorsal limiting elevations; a lateral ridge on each side of latter gradually disappearing anteriorly; posteriorly, lateral ridges ascending to pointed, short, dorsal projections; a posterior ridge extending from the latter ventrally, fusing with its fellow of the opposite side midventrally at the longer, unpaired, median posterior projection; projections prominent in lateral view; a deep lateral groove, or a wide depression as shown by Brooks and Stiasny, gradually forming ventral and anterior to dorsal posterior projections, continuing anteriorly to the front third of body; a ventrolateral ridge extending from gut swelling, coursing anteriorly up to ventral lip; gut swelling moderately large; midventral ridge on posterior region of gut swelling; midventral depression coursing anteriorly from this to base of lower lip; this depression raised slightly in cross section, limited on each side by deep grooves; ventrolateral elevation bearing a ventrolateral ridge (which may be weak)

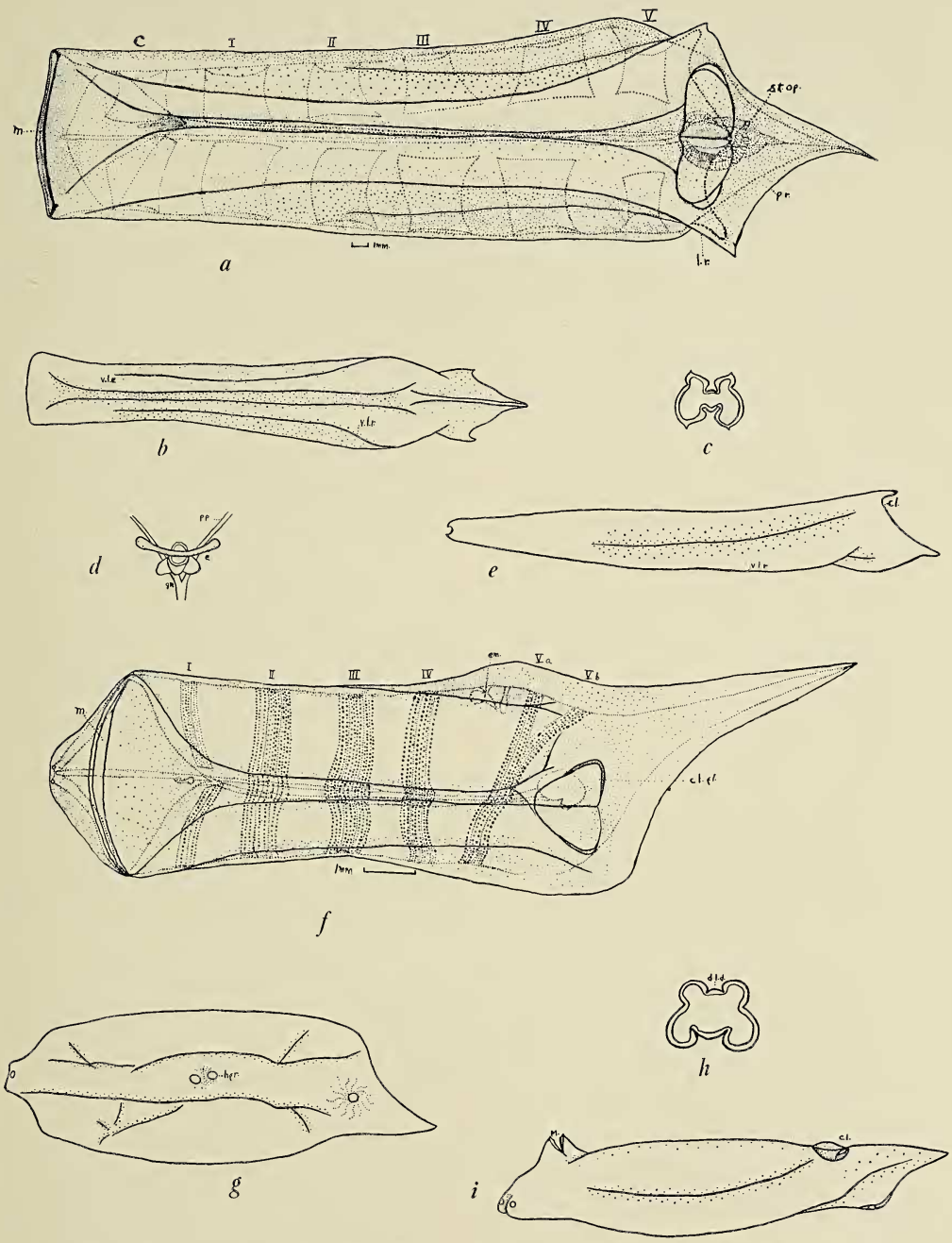


FIG. 30. *Iasis zonaria*. *a*, Solitary form, dorsal aspect; *b*, same specimen, ventral surface of test; *c*, same specimen, schematic cross section of test at level of M III; *d*, another specimen, dorsal aspect of eye and ganglion; *e*, same specimen as *a*, test, left side; *f*, aggregate form, dorsal aspect; *g*, another specimen, test, ventral surface; *h*, schematic cross section of test at level of M IV; *i*, same specimen as *g*, test, left side.

swinging outward at level of gut swelling and inward toward anterior third of body; cloacal flap of two fused halves, fringed as in *Thalia democratica;* transverse groove anteriorly at base of flap, posteriorly around cloacal opening. *Muscles:* M C and the five body muscles are broad; all muscles interrupted dorsally and ventrally; M V relatively narrow, extending only a short distance toward ventral surface. *Ciliated groove, ganglion and eye:* Ciliated groove simple, straight, located between the two bow muscles; ganglion and eye between M C and M I; eye may be transversely elongate (Fig. 30*d*). *Viscera:* Gut in condition D of Ihle and Ihle-Landenberg (1933); stolon forming circle around gut, opening to outside of test by means of a posterior opening just above gut (small in Fig. 30*a* but may be much larger).

AGGREGATE FORM: More than 10 specimens examined with length range of 19–37 mm. (Fig. 30*f–i*). *Test:* Asymmetric; consistency as in solitary form; dorsal depression (raised in cross section) with deep groove on each side but without fine median ridge described by Stiasny (1926), extending to base of upper lip; dorsal limiting elevations may bear a weak ridge on each side of depression; anteriorly both lips project dorsally prominently; a prominent chin forming anterior to lower lip; laterally a deep lateral groove (often a broad depression) extending from region of cloacal flap to level of mouth (weak ridges may course above and below this); lips and chin prominent in lateral view; ventrolateral elevation extending posteriorly as a ridge onto posterior projection; gut swelling prominent; on ventral surface, a broad, raised in cross section, midventral depression with a deep groove on each side, extending to chin; limited by ventrolateral elevations; rear projection always on right side, usually long but may be short; a broad, long mantle process extending into posterior projection; attachment organs prominent; two anteriorly directed, one ventrally directed on chin; two midventral, raised on an elevation; three posterior, raised on an elevation of gut swelling. The number described is the maximum number as reported by Streiff (1908) and Stiasny (1926). Some individuals may deviate from this maximum (Fig. 30*g*). Further, Stiasny shows two prominent lateral ridges rather than a single lateral groove. He also shows prominent dorsal ridges ("Crista") which are usually only rounded elevations on the specimens examined here, but in general his description is applicable. *Muscles:* Five body muscles (M C is not shown in figure); all interrupted ventrally, M I interrupted dorsally as well; M V dividing into two branches on right side, remaining single on left. *Ciliated groove:* Simple, anterior to M I. *Viscera:* Gut compact, in condition F of Ihle and Ihle-Landenberg (1933); testis projecting as lobules around gut; up to five embryos present dorsally on right between M IV and V.

This species is morphologically one of the best-known salps as its test has a different refractive index than water, even though it is transparent. The test has been figured well by Brooks (1893) and Stiasny (1926) and described in detail by Stiasny.

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